A Phylogenetic Analysis of the Hyperoliidae (Anura): Treefrogs of Africa, Madagascar, and the Seychelles Islands

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INTRODUCTION

The hyperoliid treefrogs of Africa, Madagascar, and the Seychelles Islands are a fascinating, colorful, and diverse group. Although they are nearly as varied as the treefrogs of the Neotropics, they are less numerous; approximately 219 species are presently recognized. Adults range in body size from the diminutive, high-altitude, 15-mm-long reed frog, *Hyperolius minutissimus*, to the West African arboreal *Leptopelis macrotis* (84 mm). Most species are arboreal; however, there are terrestrial savanna species (most members of the genus *Kassina*), terrestrial highland grass dwellers (*Chrysobatrachus*), rock dwellers (*K. parkeri*), inhabitants of floating vegetation (*Cryptothylax*), and fossorial forms (*Leptopelis bufonides, L. bocagei*, and perhaps *Kassina fusca* and *K. wealei*).

Most African treefrogs inhabit the tropics, wherein the species attain the greatest diversity, especially in West Africa. Representatives are present on the tip of the Cape of Good Hope and as far north as the arid, semidesert regions of southern Niger (*Kassina fusca*) and the Somali Horn (*K. parkeri*).

Many species are brilliantly marked with stripes, saddles, and blotches of contrasting colors (e.g., many species of *Hyperolius*, terrestrial species of *Kassina*, some *Afrixalus, Kassinula*, and *Heterixalus*); others are fairly uniform in coloration (e.g., *Kassina fusca, K. kuvangensis*, most *Leptopelis, Tachycnemis, Cryptothylax, Acanthixalus*, and *Opisthothylax*). Some species exhibit "flash patches"—areas of contrasting and perhaps disruptive color (usually red or yellow) most often on the posterior surfaces of the thigh or in the inguinal region (*Tornierella, Phlyctimantis*, some arboreal *Kassina*, some *Hyperolius*).

Reproductively, African treefrogs are quite diverse. Although direct development has not been observed, hyperoliids exhibit a broad spectrum of egg deposition sites, including glued leaf nests (*Afrixalus, Opisthothylax*), holes in trees (*Acanthixalus*), holes dug in the ground (*Leptopelis*, and sometimes *Tachycnemis*), as well as the more familiar aquatic sites (some *Hyperolius, Kassina, Tornierella*). Tadpoles are varied morphologically, and some are capable of terrestrial locomotion (*Leptopelis*). Adult frogs of one montane species, *Chrysobatrachus cupreonitens*, exhibit inguinal amplexus (Laurent 1964), a phenomenon observed elsewhere in Africa only among the aquatic Pipidae and in *Nectophrynoides*. In still another, *Hyperolius obstetricans*, parental care has been documented (Amiet 1974b).

During the past three decades, considerable effort has been exerted toward elucidating the natural history and relationships of anuran groups in the Neotropics (for instance, see Duellman 1970, 1979); yet at the familial level, the treefrogs of Africa have remained largely untreated systematically. A number of excellent regional faunal studies have included hyperoliids: Guibé and Lamotte on Mt. Nimba, Liberia (1958); Schiøtz on Nigeria (1963); Perret on Cameroun (1960, 1966); Poynton (1964), Wager (1965), and Passmore and Carruthers (1979) on South Africa; Stewart on Malawi (1967); Broadley on Zambia (1971); and Guibé on Madagascar (1978). To this list must be added the detailed, valuable reports resulting from explorations of the national parks in Zaire, formerly the Belgian Congo (de Witte 1941; Laurent 1950, 1972; Schmidt and Inger 1959).

Of the various systematic revisions that have been published, among the most important are those of Laurent (1944) and Laurent and Combaz (1950), which dealt with the thorny problems of the polytypic, hyperinclusive genera *Megalixalus* and *Hylambates*. Hoffman revised the genus *Kassina* in 1942. More recently, Schiøtz treated the *Hyperolius viridiflavus* complex (1971) and the *Afrixalus* of East Africa (1974); Laurent also treated the *H. viridiflavus* complex (1976), and Largen revised the genera *Afrixalus* (1974), *Kassina* (1975), and *Leptopelis* (1977) of Ethiopia. Perret (1958a & b, 1960) published studies of

Leptopelis, *Kassina* and *Afrixalus* of Cameroun. J.-L. Amiet continues to add to the knowledge of hyperoliids of Cameroun through faunal studies (1975, 1978), analysis of mating calls (Amiet and Schiøtz 1974) and observations and descriptions of various species, such as *Opisthothylax* (1974), and *Hyperolius* (1974b, 1976, 1978, 1979).

Of special note are the two bench-mark studies by Arne Schiøtz: *The Treefrogs (Rhacophoridae) of West Africa* (1967), and *The Treefrogs of East Africa* (1975). Based on field and laboratory studies of mating calls and ontogenetic color-pattern polymorphism (a characteristic of *Hyperolius*), Schiøtz delineated the majority of treefrog species of much of equatorial Africa, exclusive of the Congo Basin.

The concept of the family Hyperoliidae, which encompasses all of the treefrogs of Africa (excluding the rhacophorid foam-nest builder, *Chiromantis*), the Seychelles, and some of those inhabiting Madagascar (*Heterixalus*) is a fairly recent one. R. F. Laurent has been the most prolific worker on African treefrogs in recent decades. He originally described the family Hyperoliidae (1951a), distinguishing it from the ranids, based primarily on the presence of a cartilaginous metasternum and unfused carpals in the hyperoliids. He also referred the Asian and some Malagasy treefrogs (rhacophorines, mantellines) to subfamilial status within the Ranidae. In addition to the arboreal African and Seychelles treefrogs (and *Heterixalus* of Madagascar), Laurent included in the Hyperoliidae a number of nonarboreal forms that are usually considered ranids—i.e., the fossorial Hemisinae, the largely terrestrial Arthroleptinae and Astylosterninae, and the Scaphiophryninae of Madagascar. Subsequently, the Scaphiophryninae has been placed in the Ranidae (Dowling and Duellman 1979) and in the Microhylidae (Guibé 1978; Laurent 1979). Laurent (1979) maintained that the Asian and Malagasy treefrogs (Rhacophorinae, in part) are a subfamily of the Ranidae, and that the family Hyperoliidae should include the terrestrial artholeptines and astylosternines. He suggested that the hyperoliids and arthroleptines were derived from astylosternine stock (1978). He placed the genus *Hemisus* in its own family, the Hemisidae (1979).

The most comprehensive systematic treatment of Old World treefrogs since Ahl's (1931) is that of S. S. Liem (1970). On the basis of data from 36 myological, osteological, cartilaginous, and external characters, Liem recognized three families: the Ranidae, Rhacophoridae, and Hyperoliidae. Liem distinguished hyperoliids and rhacophorids on the basis of 18 character states and suggested that both families were derived from the Ranidae. He suggested that the hyperoliids and rhacophorids were diphyletic, derived from two different stocks of primitive ranids. Liem's treatment of the Rhacophoridae (*sensu* Liem) is the most comprehensive to date. He examined 73 species of 10 of the 14 genera presently recognized. With regard to the Hyperoliidae, however, his material was rather scanty, both in terms of species examined and genera represented (see Materials and Methods).

Liem recognized 14 genera within the Hyperoliidae: *Acanthixalus* Laurent, *Afrixalus* Laurent, *Callixalus* Laurent, *Chrysobatrachus* Laurent, *Cryptothylax* Laurent and Combaz, *Dendrobatorana* Ahl, *Heterixalus* Laurent, *Hylambates* A. Duméril, *Hyperolius* Rapp, *Kassina* Girard, *Leptopelis* Günther (=*Tachycnemis* Fitzinger), *Megalixalus* Günther, *Opisthothylax* Perret, and *Phlyctimantis* Laurent and Combaz. He referred the Arthroleptinae and Astylosterninae to the Ranidae, but agreed with Laurent's suggestion of astylosternine ancestry for the hyperoliids. Liem examined limited samples representing eight of the genera listed above. *Acanthixalus*, *Callixalus*, *Chrysobatrachus*, *Dendrobatorana*, *Megalixalus* (=*Tachycnemis*) and *Opisthothylax* were omitted. Since the publication of his work, *Hylambates* has been suppressed in favor of *Kassina*, at the request of Laurent and Smith (1966). *Dendrobatorana* is known from a single Nigerian specimen deposited in the Zoologisches Museum, Berlin. In the original description of the genus, Ahl (1926) described the sternum as "*mit schlankem, knochernem Stiel*"; possession of a bony metasternum suggests that *Dendrobatorana* is a member of the Ranidae or Rhacophoridae and cannot be included among the hyperoliids. Drewes and Roth (1981) resurrected the genus *Tornierella* Ahl to include two endemic species from the Ethiopian highlands.

Through the kindness of numerous colleagues, it has been possible for me to study representatives of all of the presently recognized hyperoliid genera. The purposes of this study were to (1) test the hypothesis that the Hyperoliidae is a monophyletic group after inclusion of the genera omitted by Liem (1970), (2) add to and refine the definition of the family, (3) assess the intrageneric relationships of the group, and (4) examine the relationship of the arthroleptine and astylosternine ranids to the hyperoliids, in order to determine, if possible, whether Laurent (1979) is correct in including them among the Hyperoliidae.

Liem's (1970) detailed taxonomic history of Old World treefrogs is reflected in part in the following generic synonymies.

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Materials and Methods

This study is based on the examination of 1557 hyperoliid specimens. Appendix A is a list of only that outgroup and hyperoliid material examined for myological and osteological characteristics. A supplementary list of all material examined (other than that in the CAS collections, or approximately 50%) is on file in the Department of Herpetology of the California Academy of Sciences (CAS).

Specimens were double-stained and cleared using a slightly modified version of the technique described by Dingerkuis and Uhler (1977). Modifications of concentrations and time in solution varied according to the age and state of preservation of each specimen; however, incubation at 34°C during trypsin maceration significantly reduced the time required to complete the process. Examination of dissections was greatly aided by the use of the Weigert's Lugol muscle stain reported by Bock and Shear (1972). Gross measurements were made with needle-tipped calipers; fine measurements were made under either dissecting or compound microscopes with a rotating drum micrometer. Six- to ten-micron paraffin sections of vocal sac apertures, intercalary elements, and topical glands were made at CAS, University of Colorado School of Medicine (Boulder), and the Department of Anatomy, Stanford University, and routinely stained with hematoxylin/eosin and Mallory trichrome, following the procedures outlined by Humason (1972). Photographs (35-mm color transparencies) of cleared and stained specimens were taken using a zoom microscope with photographic attachment at the Museum of Vertebrate Zoology, University of California, Berkeley. Additional photographs of sectioned material were taken at CAS. All skeletal and cleared-and-stained material examined was prepared at CAS, as were all X-rays.

I adopt the terminology of Kesteven (1944) for gular musculature, Starrett (1968) for jaw musculature, Dunlap (1960) for muscles of the thigh, Trewavas (1933) for elements of the hyoid apparatus, and Trueb (1973) for osteological terms.

I employ an inverted form of the larval tooth formulae in Schiøtz (1967, 1975). According to Schiøtz, the formula for a *Kassina senegalensis* tadpole would be illustrated:

$$\frac{1}{1+1}$$
$$1$$

In this study, the same formula is expressed as 1/1+1,1.

Abbreviations used in the text follow the museum acronyms list formalized by Duellman et al. (1978).

Selection of material. Although 14 of the 36 characters Liem considered were osteological, he examined only 24 skeletons of 20 species of 6 hyperoliid genera. The material for his muscle dissections was much more broadly based, representing all of the hyperoliid material he examined.

In addition to the hyperoliids examined by Liem, I examined the following monotypic genera: *Acanthixalus, Callixalus, Chrysobatrachus, Tachycnemis* and *Opisthothylax.* Additionally, 8 species of *Hyperolius* were included, 2 of *Heterixalus,* 4 of *Afrixalus,* 16 of *Kassina,* 1 of *Phlyctimantis,* and 7 of *Leptopelis.*

Currently, the Hyperoliidae is included within the superfamily Ranoidea (Dowling and Duellman 1978), as is the Rhacophoridae. The close relationship of both families to the Ranidae was demonstrated by Inger (1967), Liem (1970), and Duellman (1975). A ranid origin for the Hyperoliidae (and also the Rhacophoridae) was suggested by Laurent (1951b), Inger (1976), Liem (1970), Duellman (1975), and Laurent (1979a). Therefore, outgroup material was selected largely from among species of the Ranidae. Unfortunately, there are no truly arboreal African ranids (except perhaps *Hylarana*), and thus the two groups are not directly comparable functionally or ecologically. In spite of this disparity, African ranids were chosen for the reason given above and also because so little is known of their anatomy. A more obvious choice might have been the Asian rhacophorids, which are ecological and functional analogs. However, since Liem's treatment of the Rhacophoridae was so comprehensive, few rhacophorid species were examined, except for certain specific characters. Where considered for comparison, these species are cited in appropriate places in the following text.

Liem (1970) examined 62 species of ranid frogs, of which 16 (representing 11 genera) were African; most of his ranid material was of oriental or Australian distribution. Furthermore, Liem examined only two skeletons of these species—one of *Astylosternus occidentalis* and one of *Dicroglossus occipitalis.* The species in the outgroup listed in Appendix A are predominantly African ranids, selected to supplement our data base for the group for the characters treated here, especially the cartilaginous characters. As stated above, several rhacophorid species (*Chiromantis, Philautis, Polypedates, Mantidactylus*), and also hylid, pseudid, and microhylid species were examined for certain specific characters. These species are not listed in Appendix A, but rather in the text where appropriate.

Savage (1973) stated "This family [the Ranidae] is so clearly African in origin, diversification and radiation that no one has seriously questioned these propositions. . . ." Moreover, on the bases of electrophoretic and immunochemical studies, it has been suggested that divergences of lines within the Ranidae, and even within the genus *Rana,* may have occurred as much as 100 million years ago (Salthe and Kaplan 1966; Wallace et al. 1971, 1973; Case 1978a, b.) Thus, because many of the African species are highly derived and their relationships poorly understood, their use as comparative material could lead to misassignment of polarity in the analysis of character states. To reduce this possibility of error, I have included as many different African genera as were available and added seven extra-African species of ranids, six of which are considered generalized: *Rana cyanophlyctis, R. palmipes, R. pipiens, R. ridibunda, R. sylvatica,* and *R. temporaria.* These species were chosen because they (1) are of medium size; (2) exhibit broad habitat utilization; (3) have extensive geographical ranges relative to other ranid species; (4) have a typical ranid breeding strategy (as described by Salthe and Mecham 1974); and (5) have unspecialized tadpoles. Clarke (1981) considered the species of African *Rana* that he examined to be related most closely to *R. temporaria* of Europe. In contrast, Wallace et al. (1973), basing their conclusions on biochemical data, considered *R. temporaria* to be related most closely to a group of western Nearctic *Rana. Rana aurora* was among this Nearctic group, thus I have included it in this study as the seventh extra-African species.

Selection of characters. Large series of hyperoliid frogs are uncommon in museum collections, thus my study suffers from the problems accompanying small sample size. Consequently, the characters chosen for analysis were those showing the least variation (where testable). I examined several of the structures utilized by Liem (1970) (e.g., palmaris complex, sphenethmoids, pupil shape, elements of the hyoid), partly to determine whether they were still useful after inclusion of genera not examined by Liem. Additionally, many of these structures appeared to be intragenerically invariable and were thus considered to be of value in estimating generic relationships. Structures of this nature, which have not been used previously in studies of hyperoliid frogs, were examined. These included digital sesamoids, vertebral centra, neural arches, and vocal sac musculature.

Structures that vary interspecifically, such as the tympanum, the hyoid, the quadratojugal, and some characters of the vertebral column, were included to elucidate relationships between species, especially within the genera *Leptopelis, Kassina, Hyperolius,* and *Afrixalus.*

Assessment of polarity. The criteria upon which I have based my assessment of the polarity of the character states examined are essentially a combination of those used by Liem (1970) and Clarke (1981) but best expressed by Kavanaugh (1978). They are listed here in order of the confidence I place in them.

1. Outgroup comparison. Character states that are broadly distributed in the outgroup (the presumptive ancestral stock) are considered primitive, as are states common in those anuran families considered primitive.

2. Character correlation. The polarity of character states not readily inferred by outgroup comparison (often complex, multistate characters) may be inferred by correlation with the polarities of characters already assessed through outgroup comparison.

3. Correlation with adaptive significance. Where the adaptive significance of a character can be inferred, the direction of change of its various states is assessed as going from the most primitive to the most highly derived through the least complex, most parsimonious evolutionary route.

4. Commonality. In characters that are apparently unique to the hyperoliids and thus not amenable to outgroup comparisons, or in characters that cannot be confidently assessed by any of the above criteria, that state most commonly present is considered primitive, since its frequency is unlikely to be due to evolutionary convergence (the commonality principle of Schaeffer et al. 1972).

Analysis. The character states were analyzed and a phenogram was generated on the CDC computer at the University of California, Berkeley, employing an agglomerative clustering program written by W. Wayne Moss of the Academy of Natural Sciences, Philadelphia. The results of the analysis (on file at CAS) indicated that the taxa examined all fell within the appropriate genera recognized by Liem (1970) and in the present study.

A cladogram of hypothetical phylogenetic relationships was generated by hand, following the principles of Hennig (1966) and utilizing a matching technique being developed by D. H. Kavanaugh of CAS. In the analytic process, when two or more cladograms were found to be equally parsimonious, attention was focused on the discordant characters, and these were reinterpreted according to the character-weighting scheme of Hecht (1976) and Hecht and Edwards (1977). That is, discordance in low-weight characters was ignored, and in high-weight characters was emphasized.

In assessing relationships among the outgroup, I was aided by a recent work on African ranine ranids by Clarke (1981). Although he treated many characters that are different from those in this study, I have assumed that those genera in which he found the largest number of primitive characters are primitive ranines. These include *Dicroglossus, Conraua, Tomopterna, Rana, Hylarana, Aubria,* and *Strongylopus.* Representatives of all of the genera he examined have been included in the outgroup here, with the exception of *Hildebrandtia.* My adherence to the hand-generated analysis does not reflect a mistrust or ignorance of computers but rather the sense of confidence that accompanies treating each dichotomy and step personally.

Characters and Character States

Each character and the polarities of its states were analyzed and employed in a cladistic analysis. A table of observed character states is given in Appendix B. Four character states examined represent synapomorphies or symplesiomorphies within the Hyperoliidae (presence of cartilaginous metasterna, unfused condition of carpals and tarsals, absence of the m. cutaneous pectoris). These character states, labelled 25, 26, 27, and 28 respectively, were utilized in the assessment of familial relationships.

1. Dorsal exposure of the sphenethmoid. Trueb (1973) discussed the extremes of ossification of the sphenethmoid. In a number of hyperoliid genera, the sphenethmoid invades the planum antorbitale, anterior to the vertical plane of the palatines. Dorsally, the sphenethmoid is visible in some species due to extensive anterior invasion and also due to the configuration of the nasals and frontoparietals. For instance, in the genera *Leptopelis* and *Tachycnemis* (the largest hyperoliids), the nasals are widely separated and the space between them is ossified. In addition, the anterior ends of the frontoparietals diverge, exposing an area of sphenethmoid which sometimes equals more than 50% of the length of the frontoparietals. In other species (e.g., *Kassina* spp.) the anterior ends of the frontoparietals converge; because they are slightly narrower anteriorly than posteriorly, the sphenethmoid is exposed laterally as well as medially (Fig. 2A).

In other hyperoliids, the sphenethmoid is barely visible in dorsal view. Trueb (1973) suggested that reduction in ossification in smaller forms may be an adaptation to lighten the skull at the expense of protection for the brain.

Four states of sphenethmoidal exposure are recognized in the hyperoliids examined:

State 0. Sphenethmoid invisible dorsally, or barely visible
State 1. Dorsal sphenethmoidal exposure equal to 0.1 to 0.2 of length of frontoparietals (Fig. 1B)
State 2. Dorsal sphenethmoidal exposure equal to 0.3 to 0.5 of length of frontoparietals
State 3. Dorsal sphenethmoidal exposure equal to 0.6 or more of length of frontoparietals (Fig. 1A)

Direction of change. Liem found that the most common state among the ranids was state 1 and regarded it as primitive. Such is the case in the outgroup examined here, and I concur with his conclusion, by outgroup comparison. Therefore, state 1 is considered primitive and state 0 and

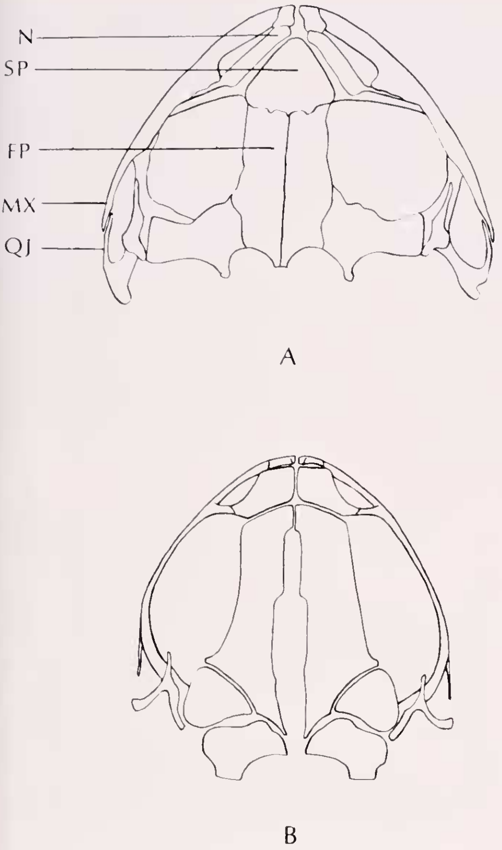

FIGURE 1. Schematic dorsal views of skulls of A) *Leptopelis bocagei* (CAS 141455), and B) *Afrixalus brachycnemis* (CAS 148400) specimens. Key: N, nasal; SP, sphenethmoid; FP, frontoparietal; MX, maxilla; QJ, quadratojugal.

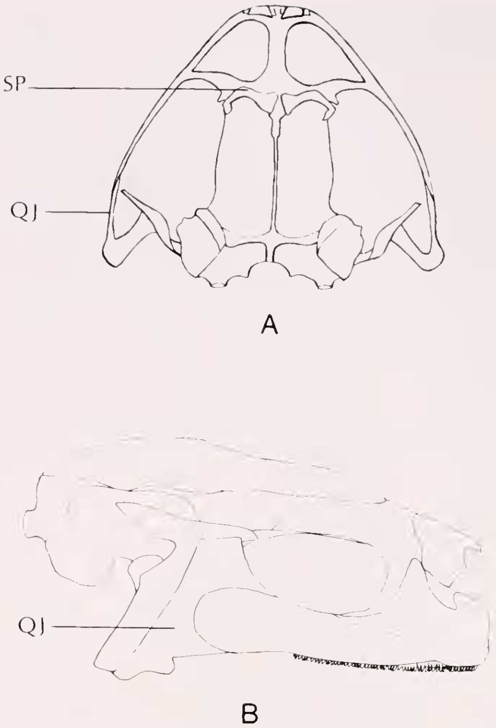

FIGURE 2. Schematic dorsal view of skull of A) *Opisthothylax immaculatus* (TNHC 38700) and B) schematic lateral view of skull of *Tornierella obscura* (CAS 141894). Key as in Fig. 1.

states 2 and 3 represent two separate lineages derived from state 1. The direction of change may be visualized as:

$$0 \leftarrow 1 \rightarrow 2 \rightarrow 3$$

2. Ventral configuration of the sphenethmoid. The sphenethmoid is an endochondral element that encloses the anterior portion of the brain and the posterior ends of the nasal chambers. In the hyperoliids examined, the sphenethmoid is either unfused, appearing paired ventrally or fused, as a continuous bony plate. Trueb (1973) warned that all sphenethmoids pass through a paired state ontogenetically and suggested that the paired sphenethmoids present in the microhylids and pipids probably reflected reduced ossification. However, the fact that a character state may be paedomorphic does not, in my opinion, invalidate it as a useful taxonomic character. In one subadult specimen of *Phlyctimantis leonardi* (MCZ 21688, snout-vent length = 33.2 mm) I examined, the sphenethmoid was paired in appearance, whereas adults of the same species (40–44 mm) showed the fused state. In taxa in which multiple adult specimens were examined, the condition of the sphenethmoid was either paired or unpaired, without variation. Two character states are thus recognized:

State 0. Ventroanterior portion of sphenethmoid a single bony plate
State 1. Ventroanterior portion of sphenethmoid unfused, consisting of two elements

Direction of change. Because state 0 was present in all ranids examined by Liem (1970) and in those I examined (except *Schoutedenella* and *Hylarana*), I considered it the primitive state, by outgroup comparison (criterion 1). The unfused state of the sphenethmoid is considered the result of paedomorphosis, and the direction of change can be simply expressed:

0 → 1

*3. **Quadratojugal.*** The quadratojugal is a small bone representing the most proximal element of the maxillary arch. Typically, the quadratojugal articulates anteriorly with the posterior end of the maxilla. In most frogs, the quadratojugal is small and reduced, and Trueb (1973) stated that there is a trend towards loss of this element among smaller species (although this is not the case in the small East African toads [Grandison, pers. comm.]). This character has been used previously in assessing relationships among the Leptodactylidae (Heyer 1975). I recognized four states:

State 0. Quadratojugal contacts maxilla anteriorly (Fig. 2A)
State 1. Quadratojugal in contact with maxilla as in state 0, but greatly enlarged dorsally—as high as or higher than dorsal extent of pars facialis of maxilla (Fig. 2B)
State 2. Quadratojugal present and entire, but not contacting maxilla. Viewed dorsally, quadratojugal is overlapped by posterior part of maxilla, but no contact between the two elements (Fig. 1A)
State 3. Quadratojugal reduced anteriorly, or absent (Fig. 1B)

Direction of change. State 0 is the normal condition, widely shared among the ranid frogs studied, and is considered primitive by outgroup comparison (criterion 1). State 1 is a unique derived character state rare among the anurans and exhibited among the Hyperoliidae only by *Tornierella.* States 2 and 3 appear to represent a trend toward loss among some of the hyperoliid genera. Therefore, the direction of change can be visualized as:

1 ← 0 → 2 → 3

*4. **Prevomerine dentigerous processes.*** Prevomers (*sensu* Trueb 1973) are paired dermal elements underlying the anterior portion of the nasal capsule. When present, the most proximal processes usually bear teeth and are known as dentigerous processes. These are usually located just anterior to the palatines (Trueb 1973). As Liem (1970) stated, edentate prevomerine odontophores are present in certain species. In the specimens I examined, two character states were found:

State 0. Prevomerine odontophore present; teeth present or absent
State 1. Prevomerine odontophore absent; prevomerine teeth always absent

Direction of change. Dentigerous processes are widespread among ranids (Liem 1970; Clarke 1981). Among those examined here, they are absent only in the arthroleptines, *Hemisus,* and the phrynobatrachines. Therefore state 0 is considered primitive by outgroup comparison (criterion 1). The direction of change can be indicated simply:

0 → 1

*5. **Vertebral centra.*** Liem (1970) utilized the nature of the vertebral centra in his analysis and found that the majority of rhacophorid frogs he examined (37 of 54 species) exhibited the procoelous condition. (Prior to Liem's work, the Rhacophoridae were generally considered to be diplasiocoelous.) Liem characterized the Hyperoliidae in part as "vertebral column always diplasiocoelous"; however, such is not the case. Two states of this character are recognized in hyperoliid frogs:

State 0. Vertebrae diplasiocoelous
State 1. Vertebrae procoelous (Fig. 3C)

Direction of change. All ranids I examined have diplasiocoelous vertebrae except the Arthroleptinae and Astylosterninae. All arthroleptines examined were procoelous (also reported by Laurent 1940b). Of the astylosternines examined, *Trichobatrachus robustus* was procoelous (Laurent 1952b) but *Astylosternus* exhibited a strange configuration that I was unable to interpret and did not include in the analysis. In these, the area of articulation between the last vertebra and the sacrum is neither concave nor convex; it is flat. In light of the frequency of its appearance in the outgroup and also the Hyperoliidae, I considered the diplasiocoelous condition primitive (criterion 1). The direction of change may be illustrated as:

0 → 1

*6. **Neural arch.*** According to Trueb (1973), the neural arches of the vertebrae of most Anura are

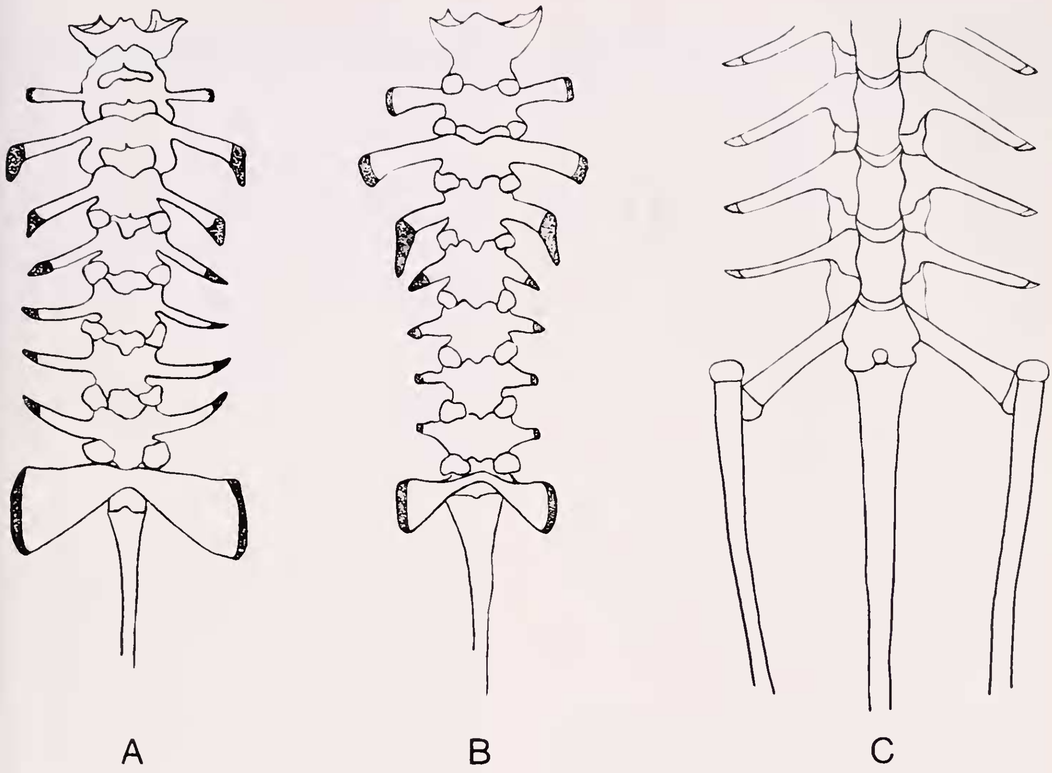

FIGURE 3. Vertebral columns. A) dorsal aspect of *Opisthothylax immaculatus* (BM 1903.7.28.42), B) dorsal aspect of *Tornierella kouniensis* (CAS 141895), and C) ventral view of posterior portion of vertebral column of *Acanthixalus spinosus* (MHNG 1034.14) illustrating procoelous condition of vertebral centra.

imbricate, completely roofing the spinal canal. Lynch (1973) suggested that the degree of imbricateness of the neural arch reflects degree of ossification, but *Notaden*, an Australian myobatrachid, retains imbricate neural arches despite considerable loss of ossification. In the hyperoliidae, two conditions are observed:

State 0. Neural arches of at least the anterior presacral vertebrae are imbricate, concealing the spinal canal (Fig. 3B)
State 1. Neural arches nonimbricate (Fig. 3A)

Direction of change. Among the ranids studied, all of the Raninae except *Rana aurora* and *Strongylopus fasciatus*, have imbricate neural arches, as does *Hemisus*. All of the arthroleptines, astylosternines, and phrynobatrachines have nonimbricate neural arches, as do the few rhacophorid species examined for this character (viz *Chiromantis petersi, Mantidactylus ulcerosus, Philautus acutirostris, P. lissobrachius, P. variabilis,* and *Polypedates leucomystax*). The broad distribution of state 0 among anurans (Trueb 1973) and ranids I studied suggests that this character state is the primitive one (criterion 1), thus the direction of change is:

0 → 1

7. Relative length of vertebral column. Lynch (1971), summarizing a number of authors, stated that the shortening of the transverse processes of the anterior presacral vertebrae and the concomitant lengthening of the transverse processes of the posterior presacral vertebrae appeared to be an evolutionary trend among frogs, but that in leptodactyloids, these lengths seemed to vary independently. Among the Hyperoliidae, there is a tendency among the more arboreal species examined toward reduction in the length of the transverse processes of the posterior vertebrae, and a lengthening of those of the fourth presacral vertebra. Regarding Lynch's statement, it must be noted that most leptodactyloid frogs are terrestrial. In some species of *Afrixalus,* in *Kassina cochranae,* and in *Phlyctimantis leonardi,* the transverse processes of the eighth vertebra are a little less than two-thirds as long as the sacral diapophyses; in *Tornierella,* they are less than half as long. This reduction is interpreted as a mechanism for decreasing rigidity of the vertebral column, allowing increased lateral mobility of the trunk. The adaptive advantage of such mobility to arboreal frogs, which are often active on surfaces of limited area such as sedges and reeds, seems obvious. The drawing of *Hyperolius puncticulatus* in Stewart (1967, p. 133) illustrates the torsion possible in hyperoliids, and I have observed this yaw in the field, which can be accompanied by upward pitch of the head so that the frog seems to be looking over its shoulder. The best way to express the dimensions of the vertebral column seems to be as the ratio of vertebral column length to greatest width of the transverse processes of the eighth vertebra, as in Liem's character 18 (1970, p. 32). My measurements include the cartilaginous epiphyses of the transverse processes; in species for which more than one specimen was examined, a mean of the values was taken and included in the analysis. The values were plotted in a frequency table, and each grouping was defined as a state of the character. As in character 8, there is some doubt regarding the inclusion of this character because of the variability in transverse processes discovered by Trueb (1977); however, although the material available to me has been limited, I have not observed comparable variability among hyperoliids. The measurements made here all fall within the range of Liem's states 0 and 2 of his character 18 (1970). I recognize three character states:

State 0. Ratio of vertebral column length to eighth transverse process length 1.6 to 2.4
State 1. Ratio of 2.5 to 3.5
State 2. Ratio greater than 3.6

Direction of change. Liem stated that the majority of ranids he examined fell into state 0; i.e., they possessed longer transverse processes relative to the vertebral column length. All of the ratios derived in my study fall within or are greater than those of Liem's state 0. State 0 is presumed primitive through outgroup comparison (criterion 1), and the direction of change can be shown as:

0 → 1 → 2

8. Orientation of transverse processes of eighth presacral vertebra. The transverse processes serve as points of origin for the many slips of the m. iliolumbaris, which insert on various portions of the ilia of the pelvic girdle (Gaupp 1896). There is a tendency among a number of hyperoliids toward anterior orientation of the eighth, and often the seventh, transverse processes. Anterior orientation of these elements implies a lengthening of the posteriormost slips of the m. iliolumbaris which originate on them, and this, along with the reduction in length of the transverse processes, suggests increased lateral mobility of the trunk (see character 7). Anterior angling of the eighth transverse processes is included in this study with trepidation, as Trueb (1977) found significant variation in this character within the large series of *Hyla lanciformis* she studied, especially among males. However, she did not include the ranges of the measurements she made. Inclusion of this character is intended to be heuristic. Two character states are recognized:

State 0. Transverse processes of eighth presacral vertebra essentially perpendicular to longitudinal axis of the vertebral column (Fig. 3B, D)
State 1. Transverse processes of eighth vertebra angled markedly forward (at least 70°; Fig. 3A)

Direction of change. Most ranid species surveyed exhibit state 0. This condition is not related to size; the examples range from small species such as *Arthroleptis poecilonotus* to large ones like *Pyxicephalus adspersus.* Of three fossorial forms, *Tomopterna* and *Hemisus* exhibit state 1, whereas *Pyxicephalus adspersus* exhibits state 0. State 0 is considered primitive by outgroup comparison (criterion 1), and the direction of change is probably:

0 → 1

9. Posterolateral process of hyoid. Liem (1970) did not observe this cartilaginous process in any of the hyperoliid species he examined but cited Hoffman (1942) who found it in *Kassina wealei.*

My study indicates that this character can be found as a reduced but recognizable element in six hyperoliid genera; however, in at least one species, *K. wealei*, the character is variable (i.e., present in some specimens of a population but not in others). In many species, the posterolateral process serves as a point of attachment for the m. geniohyoideus lateralis externus superficially and the m. petrohyoideus anterior. In many anuran species that lack the process, the petrohyoideus shifts anteriorly to insert on the hyoid plate or on its lateral borders (Trewavas 1933). I recognized two character states:

State 0. Posterolateral process present (Fig. 4B, C)
State 1. Posterolateral process absent (Fig. 4A, D)

Direction of change. The presence of the posterolateral process of the hyoid is widespread among frog groups (Trewavas 1933), and it is present in all of the ranids I studied except representatives of the Arthroleptinae. The process is absent in most hyperoliid frogs including *Leptopelis,* which has been considered the most primitive genus (Liem 1970; Laurent 1979), but present in *Acanthixalus* and *Kassinula,* both highly derived species. I therefore suggest that state 1 constitutes a reversal, probably a result of paedomorphic processes, and that it is the derived state by character correlation (criterion 2). I illustrate the polarity of the character as:

0 ← 1

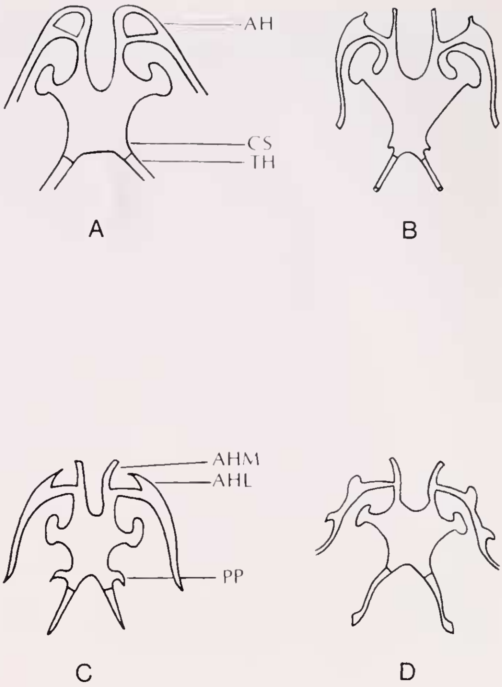

FIGURE 4. Hyoid apparati. A) *Tornierella kouniensis* (CAS 141895), B) *Acanthixalus spinosus* (MHNG 1034.14), C) *Kassinula wittei* (CAS 145846), and *Kassina fusca* (CAS 126384). Key: AH, anterior horn; AHM, medial element of anterior horn; AHL, lateral element of anterior horn; CS, cartilaginous stalk of thyrohyal; TH, thyrohyal; PP, posterolateral process. Drawn from cleared and stained specimens.

10. Cartilaginous stalk of thyrohyal. In all of the hyperoliids examined, the most proximal elements of the hyoid apparatus are the bony thyrohyals, which are widely spaced, bracket the laryngeal apparatus, and in most species are borne upon cartilaginous stalks. In many anuran species, the thyrohyals and, when present, the cartilaginous stalks, serve as points of attachment for the m. petrohyoideus posterior, the m. geniohyoideus lateralis interior, and the m. hyoglossus. Some observations in this study are not in concordance with those of Liem (1970), e.g., the presence of cartilaginous stalks among members of the genus *Leptopelis.* Two character states are recognized:

State 0. Thyrohyals abut directly on hyoid plate, not on cartilaginous stalks (Fig. 5C)
State 1. Thyrohyals borne on cartilaginous stalks (Fig. 4A–D)

Direction of change. Trewavas (1933) showed that direct abutment of the thyrohyals on the hyoid plate is common among many frog groups. All of the ranid species examined here showed this condition except *Arthroleptella, Cacosternum,* and the astylosternines and arthroleptines (except *Cardioglossa*), the latter two confirming Laurent (1978). Therefore, state 0 is primitive by outgroup comparison (criterion 1); state 1 seems simply to reflect reduced ossification, is likely a paedomorphic feature, and is considered derived. The direction of change is:

0 → 1

11. Anterior horn of hyoid. The anteriormost process of the hyoid apparatus is the anterior horn. In a number of hyperoliid species, the lat-

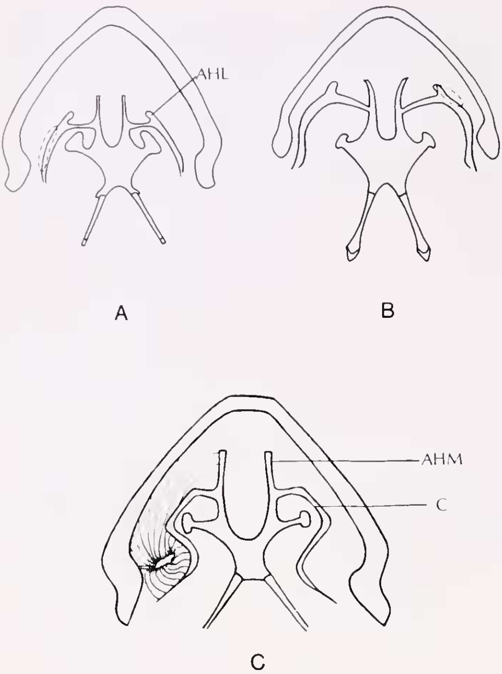

FIGURE 5. Vocal sac openings. A) *Tachycnemis seychellensis* (BM 1976.1908), B) *Kassina parkeri* (CAS 140352), and C) *Leptopelis karissimbensis* (CAS-SU 13019). Abbreviations as in Fig. 4. Dotted lines in A) and B) indicate position and size of slitlike vocal sac openings relative to the ceratohyal. C) illustrates the sphincteral opening, with slips of the m. petrohyoideus anterior delineated. Composite drawings from both cleared and stained and dissected specimens.

eral element of the anterior horn serves to form the medial margin of the vocal sac opening. Liem (1970) recognized three character states based on the shape of this process; in the present study, the following states are noted:

State 0. Anterior horn entire, forming a complete arch (Fig. 4A)
State 1. Anteriormost portion of anterior horn absent so that the horn is composed of two elements: an anteromedial process and a lateral process (Fig. 4B, C)
State 2. Lateral process of anterior horn absent (Fig. 5C)
State 3. Same as state 1, except that an additional lateral process present (Fig. 4D)

Direction of change. Among the specimens Trewavas examined (1933), the groups in which this structure (or its constituent parts) is uniformly absent are the leiopelmatids, discoglossids, and pelobatids, all of which are considered primitive or transitional; its presence is apparently rare among the Hylidae. In the microhylids, this structure may be interpreted either as present as a thin strip or flange contiguous with the ceratohyal, or absent.

Among the ranid material examined here, it is absent in *Hemisus, Abrana, Ptychadena anchietae* and *P. mascareniensis.* State 2 is exhibited by the Arthroleptinae, Astylosterninae, and the majority of the other ranid species studied. In most ranines (except *Hylarana*) and phrynobatrachines, the medial process is a small perforated or unperforated disc or hook-shaped process.

The function of the anterior horn of the ceratohyal is unclear, but I suspect that it is involved in the vocalization apparatus. In *Leptopelis,* it serves as a point of insertion for anterior fibres of the m. petrohyoideus anterior, which are the distalmost portions of the vocal sac openings (Fig. 5C). It may serve the same function in ranids, the majority of which have vocal sac openings similar to those in *Leptopelis.* In all hyperoliids except *Leptopelis,* the anterior horn of the ceratohyal forms the lateral margin of the usually anterior, slitlike vocal sac openings. In members of *Leptopelis,* the m. petrohyoideus anterior is not involved with the ceratohyal in this manner.

Liem (1970) suggested a trend toward reduction of the lateral element of the anterior horn in the Hyperoliidae and considered state 0 to be primitive. I suggest that the reverse is true—that there is a trend toward elaboration of the anterior horn and that this trend may be linked to the development of anterior vocal sac openings possessed by most hyperoliids. By outgroup comparison and character correlation (criteria 1, 2), state 2 is considered primitive, with states 1 and 0 reflecting the trend mentioned above. State 3 is a specialization, apparently derived from state 1, which it closely resembles. The direction of change may be indicated as:

$$\begin{tikzcd} 0 & 1 \arrow[l] \arrow[d] & 2 \arrow[l] \\ & 3 & \end{tikzcd}$$

12. Palmaris musculature. In ranids, rhacophorids, and hyperoliids, Liem (1970) recognized seven character states of the palmaris musculature, which he described in detail. These states

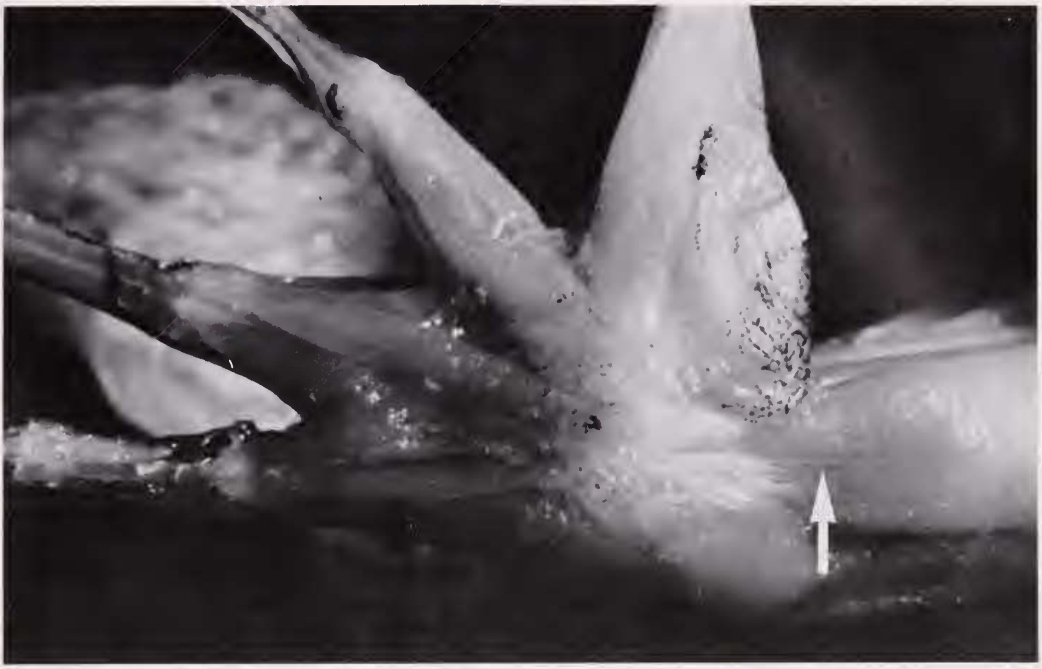

FIGURE 6. Palmar view of right hand of *Rana angolensis* (CAS 147801), illustrating state 0 of character 12. Aponeurosis palmaris is white mass in center of picture. Note that distal end of the m. palmaris longus is undivided (see arrow). Photo by John E. Simmons (CAS).

were based on (1) the divisions and insertions of the distal portions of the m. palmaris longus and m. palmaris profundus, (2) the absence or presence of the aponeurosis palmaris and the tendons and muscle slips that insert upon and/or slide through it, and (3) the position and proximal insertions of the tendenes superficialis of the fingers. I recognize three states of this complex and simplify the descriptions of these states.

State 0. (Liem state 1.) Aponeurosis palmaris present and obvious; none of the tendenes superficialis is able to slide through it—they originate upon its distal rim; distal portion of m. palmaris longus not divided, and inserts on the proximal rim of the aponeurosis palmaris (Fig. 6)

State 1. (Liem state 5.) Aponeurosis palmaris present but usually thin and diaphanous; proximal ends of third and fourth tendenes superficialis are able to slide through it, and are joined to heads of the divided m. palmaris longus (Fig. 7)

State 2. (Liem state 6.) Aponeurosis palmaris absent, but tendenes superficialis are joined with heads of divided m. palmaris longus, as in state 1 (Fig. 8)

Direction of change. All of the states of this character complex observed among the Hyperoliidae fall within one of the two diverging lineages described by Liem (1970). In all ranids he examined and also those I examined, the tendenes superficialis were unable to slide through the aponeurosis palmaris and instead originated from its distal edge. Liem suggested that the function of the aponeurosis palmaris as a sleeve through which the tendenes superficialis slide was one of the structural modifications of the palmaris complex involved in increased mobility of digits, and thus increased arboreal efficiency. State 0 is considered the primitive one. The major difference between states 1 and 2 is that in state 2 the aponeurosis palmaris is absent; independent flexion of the third and fourth digits is still possible, as the tendons are still joined with the divided m. palmaris longus. The m. palmaris

FIGURE 7. Palmar view of left hand of *Cryptothylax greshoffi* (CAS 145277) illustrating state 1 of character 12. Aponeurosis palmaris is thin, diaphanous and not clear in photo; note that distal end of m. palmaris longus is divided (arrow), and communicates through the aponeurosis palmaris with the third and fourth tendenes superficialis. Photo by John E. Simmons (CAS).

profundus, which ordinarily inserts on the lateral edge of the aponeurosis, inserts directly on the proximal portions of the third and fourth tendenes superficialis. State 2 is considered the derived condition and state 1 intermediate. Among the Hyperoliidae, the distribution of these character states is absolutely correlated with habitat (i.e., all arboreal species possess state 1, all terrestrial species possess state 2 or state 0), even within a genus (*Leptopelis, Kassina*). The direction of change can be illustrated as:

$$0 \rightarrow 1 \rightarrow 2$$

Great care must be exercised in examining members of the genus *Leptopelis* for this character, as the palmar dermis adheres closely to the aponeurosis palmaris, which is damaged easily. When this structure is damaged, state 1 can resemble state 2.

13. Digital sesamoids. Sesamoids (heterotopic elements) are mineralized areas that form within tendons where these overlie joints (Hildebrand 1974; Romer 1970). Digital sesamoids are present in some terrestrial hyperoliid species as well as in a few of the arboreal forms. They are found on the flexor surfaces of distal ends of various phalanges in the hand and foot of adults and postmetamorphic juveniles, but in the latter they are not mineralized. In the species examined, there is no correlation between presence of sesamoids and presence of large subarticular tubercles. Sesamoids occur in combinations which may be species specific, but their presence in arboreal and terrestrial forms precludes their being an adaptation to habitat. Furthermore, they are absent in many terrestrial ranid genera, such as *Phrynobatrachus.* They are present in at least one fossorial ranid, *Hemisus,* but absent in two others—*Tomopterna* and *Pyxicephalus.* The ecological significance of these elements is unknown.

FIGURE 8. Palmar view of right hand of *Kassina wealei* (CAS 125746) illustrating state 2 of character 12. Aponeurosis palmaris is absent, m. palmaris longus is divided (arrow), and m. palmaris profundus inserts on dorsal surface of tendenes superficialis. M. palmaris longus communicates directly with tendenes superficialis. Photo by John E. Simmons (CAS).

Two character states are recognized:

State 0. Sesamoids present in subarticular regions of distal ends of phalanges of some or all fingers and toes (Fig. 9)
State 1. Sesamoids absent

Direction of change. Laurent (1940) described digital sesamoids in the Arthroleptinae and subsequently (1941) he reported them as being constant in ranids and absent in rhacophorids. I can confirm their absence in the rhacophorids *Chiromantis petersi, Mantidactylus ulcerosus, Polypedates leucomystax,* and *Philautus* spp. Among the ranid species I examined, sesamoids are present in *Hemisus, Arthroleptis, Schoutedenella, Astylosternus,* and *Ptychadena oxyrhynchus,* and absent in all others studied. Thus, state 1 is considered the primitive state by outgroup comparison (criterion 1) and state 0 the derived condition. The direction of change can be illustrated as:

$$0 \leftarrow 1$$

14. Terminal phalanx of third finger. Many arboreal and some terrestrial frog species (such as *Hylarana*) exhibit expanded finger and toe tips, which presumably are supported in part by various modifications of the terminal phalanges.

FIGURE 9. Lateral view of left foot of cleared and stained *Kassina senegalensis ruandae* (CAS 111636). Arrows indicate digital subarticular sesamoids characteristic of kassinoid genera (state 0, character 13).

It might be assumed as well that these modifications of terminal phalanges are specializations for different muscle insertions. However, in spite of at least one detailed morphological study (Noble and Jaeckle 1928) and other more recent works utilizing modern techniques (e.g., Richards 1977; Green 1979; Emerson 1980), the relative functions of the intercalary elements, terminal phalanges, and in fact the toe tips themselves, remain obscure. Many systematists have used the shape of the terminal phalanx in phylogenetic constructs (Tihen 1965; Perret 1966; Liem 1970; Lynch 1971; Heyer 1975; Clarke 1981). Within the Hyperoliidae at least, the correlation between branched or expanded terminal phalanges and enlarged toe pads is suspect, for many forms with rather simple terminal phalanges, such as *Leptopelis, Hyperolius,* and *Afrixalus,* possess enlarged digital discs. It must be noted, however, that among the specimens I examined, those species with strongly bifurcated terminal phalanges also possess enlarged toe pads. I have found the terms "T-shaped" and "Y-shaped" adequate for some members of the outgroup, but not appropriate for any of the Hyperoliidae. Heyer (1975) discussed the variation of terminal phalanx shape from digit to digit. With this in mind, I made the following observations on the third phalanx, although I have noticed little variation of this character in the specimens examined. Liem (1970) recognized four states of this character; Clarke (1981) recognized seven. I recognize four character states, based on examination of cleared and double-stained specimens.

State 0. Terminal phalanx long, slender, and claw shaped; curved ventrally and tapered evenly to a point (Fig. 10B)

State 1. Terminal phalanx long and slender as in state 1, but peniform; a noticeable constriction present near tip. Tip oval, but not pointed. Phalanx may be slightly curved, but not as much as in state 1 (Fig. 10C)

State 2. Terminal phalanx short, obtuse, and unmodified or the tip slightly notched, or emarginate (Fig. 10A)

State 3. Similar to state 2, except the tip bifurcate, each branch longer than width of phalanx just proximal to bifurcation (Fig. 10D)

Direction of change. Liem (1970) said that state 0 was the most common configuration among generalized ranids, and also that modifications of the terminal phalanx were present in most arboreally adapted species. My comparative material suggests that states 0, 1, and 2 are all present in the ranids. Liem considered the claw-shaped terminal phalanx to be a specialization, as it "occurs among a few ranid groups such as the astylosterninae, arthroleptinae, and *Ptychadena.*" I agree that the state is specialized, but have found the arthroleptines and astylosternines to have state 2. State 1 is considered to be the primitive state by character correlation (criterion 2), with state 0 derived from it. States 2 and 3 are considered to represent a trend toward bifurcation among the hyperoliids. The direction of change is visualized as:

0 ← 1 → 2 → 3

15. Coracoids. All hyperoliids are firmisternal, i.e., the coracoids of the pectoral girdle meet midventrally, with no overlap of epicoracoidal cartilage as in the Arcifera. In several African ranid groups such as *Arthroleptis* and *Schoutedenella,* the coracoids are medially emarginated or bifurcate (Laurent 1973; and pers. comm.). *Hemisus* has this character state highly developed. Oxnard (1971) discussed the effect of net tension on flat bones as sometimes leading to fenestrae and replacement by fibrous material. Fenestrae occur in some hyperoliids, in which the edges of the medial perforation are smooth and uniform and do not appear to be the result of incomplete ossification. Two character states are recognized among the Hyperoliidae:

State 0. Medial margins of coracoids entire (Fig. 11A, B, D)
State 1. Medial margins of coracoids centrally perforated (Fig. 11C)

Direction of change. In most ranoid frogs (including those surveyed), the medial margins of the coracoids are entire. Perforations in the coracoids of *Arthroleptis* and *Schoutedenella,* and their remarkable bifurcation in the genus *Hemisus* are regarded as derived states, although their functional significance remains unknown. I confirm the presence of bifurcate coracoids in the Arthroleptinae except in *Arthroleptis poecilonotus* and *A. reichi,* in which they are normal. Therefore, the direction of change can be simply illustrated:

0 → 1

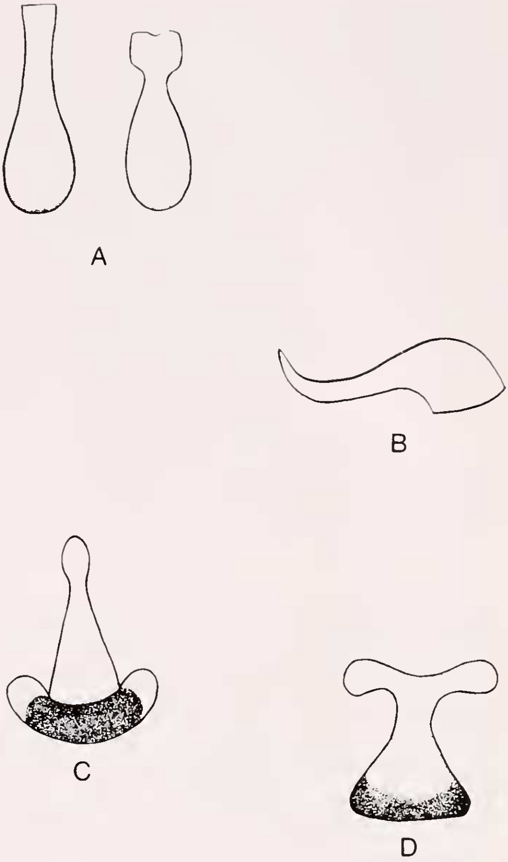

FIGURE 10. Terminal phalanges. A) *Kassina kuvangensis* (UM 28424), left, and *K. maculata* (UM 26439), right, B) *Leptopelis macrotis* (CAS 125484), C) *Tachycnemis seychellensis* (UMMZ 144312), and D) *Acanthixalus spinosus* (MHNG 1034.14).

16. Omosternum. The omosternum is the anteriormost bony element of the pectoral girdle and serves as a point of origin for the m. coracoradialis and the m. deltoideus episternalis. In most hyperoliid genera I examined, the base of the omosternum is more or less forked and, with one exception, always bony. In one adult example of *Leptopelis brevirostris,* LACM 125753, the omosternum is entirely cartilaginous, without a trace of mineralization. Forking is usually bilaterally symmetrical, but in one species, *Chrysobatrachus cupreonitens,* there is apparent sexual dimorphism; one male was coded as 1, a female was coded as 2. In the following analysis, the taxon is coded as 3. In the male, the right arm is shorter than the left, skewing the omosternum to the right as originally described by Laurent (1951); the female is symmetrical. All other species where several specimens were examined lacked such variation. Some of my observations do not agree with those of Liem (1970) for the same species. Four character states are recognized:

State 0. Base of omosternum unforked, usually forming a flat or slightly convex plane (Fig. 11A)
State 1. Omosternum notched or slightly forked,

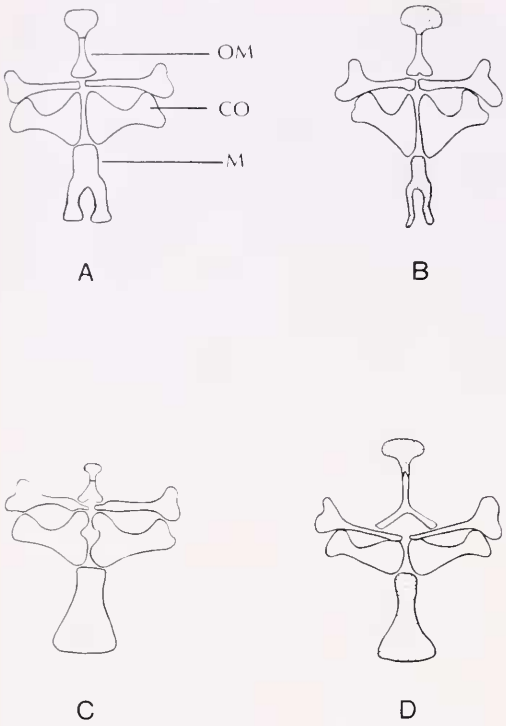

Figure 11. Pectoral apparati. A) *Leptopelis notatus* (LACM 64535), B) *Leptopelis bocagei* (CAS 141455), C) *Tornierella kouniensis,* (CAS 141895) and D) *Kassina cassinoides* (ZMUC 73864). Key: OM, omosternum; CO, coracoid; M, metasternum.

greatest space between arms less than half width of a single arm (Fig. 11B)

State 2. Omosternum moderately forked, inter-arm space one to two times width of one arm (Fig. 11C)

State 3. Omosternum greatly forked, space between arms more than twice width of one arm (Fig. 7D)

Direction of change. According to Deckert (1938), the forked condition of the omosternum is derived from the unforked; Liem (1970) stated that *Rana* possess the latter condition, although he cited the presence of states 1 and 2 in 17 additional ranid genera. My findings corroborate Liem's in *Rana* (except *R. cyanophlyctis,* which is state 3); the arthroleptines exhibit state 3 and most Phrynobatrachinae possess state 2 (in *Arthroleptella* and *Cacosternum* the structure is absent). Clarke (1981), following the principle of commonality, found state 2 the most widely distributed among ranines and treated it as primitive. Among the Hyperoliidae, there seems to be a strong trend toward increased forking of the omosternum. There are two possible interpretations of polarity for this character. If one follows Liem and assumes that *Rana* is primitive, the direction of change can be expressed as:

$$0 \rightarrow 1 \rightarrow 2 \rightarrow 3$$

If the distribution of character states among the Raninae are accepted *fide* Clarke and this study, it can be illustrated as:

$$0 \leftarrow 1 \rightarrow 2 \rightarrow 3$$

For the purposes of this analysis, the first alternative is chosen because within the Hyperoliidae, species with the most primitive condition (state 0) also exhibit other primitive characteristics (e.g., *Leptopelis*) and the most logical evolutionary sequence is from most primitive (state 0) to most derived. Thus, by character correlation, state 0 is considered primitive.

17. Metasternum. The metasternum of all hyperoliid frogs is a thin cartilaginous plate, which may be broader than or nearly as narrow as the cartilaginous area where the epicoracoids meet (see character 25). The cartilaginous nature of the metasternum may suggest a difference in the proportions of the m. pectoralis sternalis as part of the pectoral complex, a possibility as yet unstudied and beyond the scope of the present work. Several authors have noted a tendency toward mineralization among certain hyperoliid species. The staining technique used here (Dingerkuis and Uhler 1977) has revealed that there is some mineralization present in the majority of the specimens examined. However, even in these, the metasternum is clearly basically cartilaginous, thin and flattened, and in no way resembles the bony style of ranids and rhacophorids. Table 1 is a list of those species in which mineralization was observed and in which portion of the plate it occurred. In the species examined, the posteriormost margin of the metasternum appears to be uninvolved in muscle attachment, and in skinned specimens it is externally visible. Ratios of caudal width to anterior width of the metasternum were made and manipulated as those in character 7. Three character states are suggested:

State 0. Ratio of caudal margin of metasternum to anterior margin is from 0.6 to 1.4 (Fig. 11B)

TABLE 1. SPECIES OF HYPEROLIIDAE EXAMINED WITH AREAS OF MINERALIZATION IN THE METASTERNUM.

Acanthixalus spinosus—medial plate
Afrixalus brachycnemis—stem
A. congicus nigeriensis—plate, not arms
A. f. fornasini—plate, not arms
A. osorioi—plate, not arms
Callixalus pictus—mid-stem
Cryptothylax greshoffi—stem & plate
Heterixalus madagascariensis—anterior stem
Hyperolius argus—whole structure
H. castaneus—stem
H. montanus—stem
H. nasutus—stem
H. phantasticus—anterior stem
H. picturatus—stem
H. pusillus—stem
Kassina cassinoides—stem
K. cochranae—anterior stem
K. kuvangensis—stem
K. lamottei—anterior stem
K. maculatus—stem
K. mertensi—anterior stem
K. parkeri—anterior stem
K. senegalensis angeli—anterior stem
K. s. deserticola—lateral marg. stem
K. s. ruandae—stem
K. s. somalica—anterior stem
K. s. uelensis—anterior stem
K. wealei—anterior stem
Leptopelis bocagei—plate, not arms
L. boulengeri—anterior stem
L. christyi—anterior stem
L. hyloides—anterior stem
L. macrotis—plate, not arms
L. modestus—plate, not arms
L. notatus—plate, not arms
L. viridis—anterior stem
Opisthothylax immaculatus—anterior stem
Phlyctimantis verrucosus—stem
Tachycnemis seychellensis—stem

State 1. Ratio from 1.5 to 3.0 (Fig. 11C, D)
State 2. Ratio greater than 3.0

Direction of change. The majority of hyperoliid species examined (70%) fall within state 1, including some of the most highly specialized forms (based on other parameters), e.g., *Tornierella* (Drewes and Roth 1981). The commonality principle of Schaeffer et al. (1972) is invoked, and state 1 is considered the primitive condition (criterion 4). State 0 is considered to represent a trend among some species toward reduction of the metasternum, perhaps in the direction of the style condition exhibited by most ranids and rhacophorids, and state 0 is apparently independently derived from state 1. The presence of a cartilaginous metasternum in the Arthroleptinae and Astylosterninae has been noted (Laurent 1941) and is confirmed here. The direction of change is:

$$0 \leftarrow 1 \rightarrow 2$$

18. Vocal pouch and gular gland. Liem (1970) linked the development of vocal pouches of male frogs with presence or absence of gular glands. He recognized two lineages—one in which the vocal pouch evolved with the gular gland and one that developed without the gland. Although I am not convinced that this is the correct approach, I included the two together for ease of description and because in at least one hyperoliid group (*Kassina*) the gular gland may serve functionally as a replacement for the submandibular septum when this structure is absent. Furthermore, the gular gland, which is probably not distensible, may alter the shape of the expanded vocal pouch (see character 21). In the genera *Acanthixalus* and *Callixalus,* gular glands are present, but vocal sacs and pouches are absent. Similarly, in *Cryptothylax greshoffi,* the gular gland is present, but the vocal pouch absent. Moreover, in *Callixalus,* the columella is reduced and the annulus tympanicus is present merely as a remnant. If *Callixalus* falls into Liem's group within which the vocal pouch evolved in association with the gular gland, then reduction and absence of these associated structures must be secondary. An alternative hypothesis is that the gular gland evolved in these species independently of the vocal pouch.

The Hyperoliidae rival even the Leptodactylidae in distribution of topical glands (Lynch 1971). Males of most species possess topical glands, and many species have them in the gular region as well as in discrete patches in the pectoral region, on the inner surfaces of the forearms, and on the digits. In *Tornierella* there are great concentrations of glands on the posterior surfaces of the tarsi.

Table 2 is a list of the distribution of topical glands among the hyperoliid genera. Gular glands of hyperoliids have been described as "adhesive" discs (Loveridge 1925), "protective flaps"

TABLE 2. DISTRIBUTION OF TOPICAL GLANDS AMONG MALE HYPEROLIID SPECIES.

Genus	Gular Gland	Forearm Glands	Pectoral Glands	Digital Glands
Acanthixalus	X	–	–	–
Afrixalus	X	–	–	–
Callixalus	X	X	–	–
Chrysobatrachus	X	X	X	–
Cryptothylax	X	X	X	–
Heterixalus	X	–	–	–
Hyperolius	X	X	X	X
Kassina	X	X	–	X
Kassinula	X	–	–	–
Leptopelis	–	X	X	X
Opisthothylax	X	X	–	X
Phlyctimantis	X	X	–	X
Tachycnemis	X	–	–	–
Tornierella	X	X	–	X

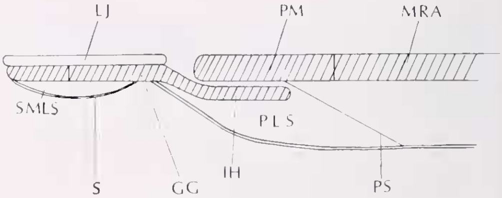

FIGURE 12. Schematic drawing of sagittal section of anterior portion of *Kassina senegalensis* showing elements of vocalization apparatus (after Tyler 1971c). Key: LJ, lower jaw (here for orientation, only); SMLS, submandibular lymph sac; S, skin of vocal pouch; GG, gular gland; PLS, pectoral lymph sac; IH, m. interhyoideus; PS, pectoral septum; PM, pectoral musculature; MRA, m. rectus abdominus. The greatly slanted pectoral septum allows for expansion of vocal sac musculature during call.

(Schiøtz 1967, 1975), and "sucker-like folds" (Power 1926); the actual function of the gular glands remains obscure. Sections of the glands of at least one specimen of all of the species studied here indicate that Trong (1976) was correct in describing the gular glands as compound and alveolar, and associated with regular mucous and serous glands (as described by Gaupp 1907). Comparison with sections of forearm glands (when present) from the same specimens suggests that the glands are very similar in structure. Trong also showed that the secretions of the gular glands in *Phlyctimantis* and *Kassina* contained no indoles or phenoles, compounds implicated by Anastasi et al. (1977) and by Montecucci et al. (1977) in the toxic properties of the dermal glands of *Kassina senegalensis* and of *K. maculata*, respectively.

I have collected many specimens of *Kassina senegalensis*, *Hyperolius* spp., and *Afrixalus* spp. in amplexus, and no "gluing" has been observed. I have pithed a number of specimens of several species of *Kassina* in the laboratory, and while such stress will cause firing of the diffuse dermal glands of the skin (a thick milky substance, especially noxious in *K. wealei*), the topical glands do not discharge. The location of the glands suggest that they are hedonic in nature. One male and one female specimen of the species *Tornierella obscura* from Dasse, Ethiopia (BM 1965.1873–4), were collected in amplexus and evidently preserved immediately (preservative unknown); the male retained a coarse brownish substance on the ventral surface of the gular gland, the inner surface of the forearm glands, on the digital glands, and on the posterior surface of the tarsus. On the female the same substance was present on all surfaces presumably in contact with the male during amplexus and also on the tarsus.

In at least one species, *Hyperolius obstetricans*, the gular gland of the male is absent (Amiet 1974); in two others, *Kassina maculata* and *Hyperolius spinigularis*, it appears only during breeding seasons (Poynton 1964; Stevens 1971). I sectioned the "gular gland" of *Hemisus* (figured in Noble 1931) and found it to be a hollow cutaneous pouch, no more glandular than dorsal skin. Its function is unknown.

Salthe and Mecham (1974) cited works showing that olfaction may be important in directing breeding aggregations to breeding sites, and Perret (1961) suggested this function for the gular gland in the hyperoliid species, *Acanthixalus spinosus*.

Members of the genera *Kassina*, *Phlyctimantis*, *Kassinula*, and *Tornierella* possess the most complex vocal pouch apparati among the Hyperoliidae. Not only the gular region but also much or most of the pectoral region is involved when the vocal pouch is inflated (see Figs. 12, 13). Furthermore, these pouches are unique in having two densely pigmented accessory areas of distensible tissue underlying the gular gland (which is round or straplike). Ordinarily, these areas are hidden from view by the gular gland. However, laboratory and field observations of some species confirm that when the vocal pouch is inflated, these pigmented elements are everted and become highly visible. Wager (1965) described these "two smaller balloons" in *Kassina*

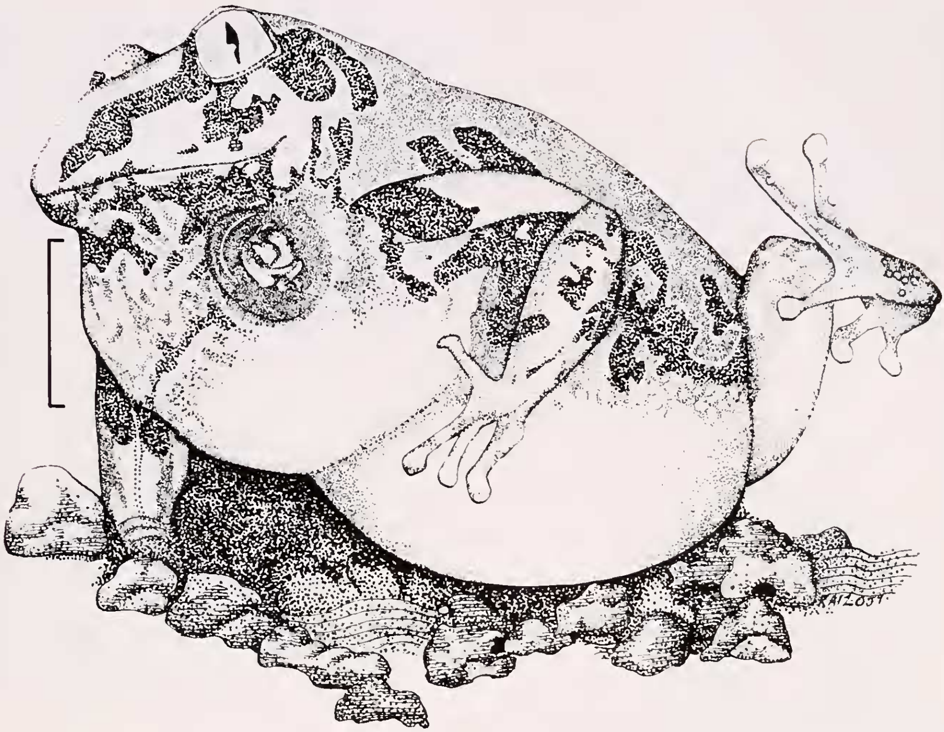

FIGURE 13. Drawing from photograph by John E. Simmons (CAS) of captive *Kassina senegalensis* which has just called. The animal has been startled, and the vocal pouch is not expanded as fully as has been seen in the field. Note the posterior extent of the vocal pouch, which intrudes into the pectoral region, and the dark tissue of the accessory pouches that underlie the gular gland. Bracket denotes vertical extent of gular gland. The positions of the left fore and hind limbs are due to the fact that the animal is leaning against the glass of a terrarium.

maculata, and Rose (1962) and Power (1925), those in *K. senegalensis*.

The functional significance of these vocal pouch structures is not known. The gular gland is probably not distensible, which perhaps accounts for the involvement of the pectoral region in *Kassina* and its allies as a means of increasing the size of the inflated vocal pouch in compensation. The black distensible areas of tissue may serve as visual cues for females and/or other males. I have frequently observed calling males of *Kassina senegalensis*, and most often, the vocal pouch is retained in the inflated condition between calls (although Wager [1965] stated that the pouch of *K. maculata* is deflated immediately after the call is made). The inflated vocal pouch gives the calling and postcall male a greatly enlarged, rather grotesque appearance, the dark areas looking very similar to the eyes of some other animal from ground level (see Fig. 13, drawn from photo). My initial hypothesis with respect to *K. senegalensis*, which calls from concealment on land, was that the vocal pouch formed an image that might serve to deter potential terrestrial predators. However, similar structures are possessed by all species of the genus, and calling sites vary considerably intraspecifically from positions in the water to arboreal sites (Rose 1962; Wager 1965; Schiøtz 1967, 1975; Channing 1976). At least in *K. senegalensis*, calling males are spaced around a water source and interact vocally (Wickler and Seibt 1974; Bowker and Bowker 1979), and it is possible that the size and shape of the male vocal pouch serves to attract females (Wilbur et al. 1978) and/or to establish breeding territory.

Eight character states of the gular gland and associated vocal pouch are recognized here:

State 0. Gular gland absent; vocal pouch absent
State 1. Paired longitudinally oval gular glands

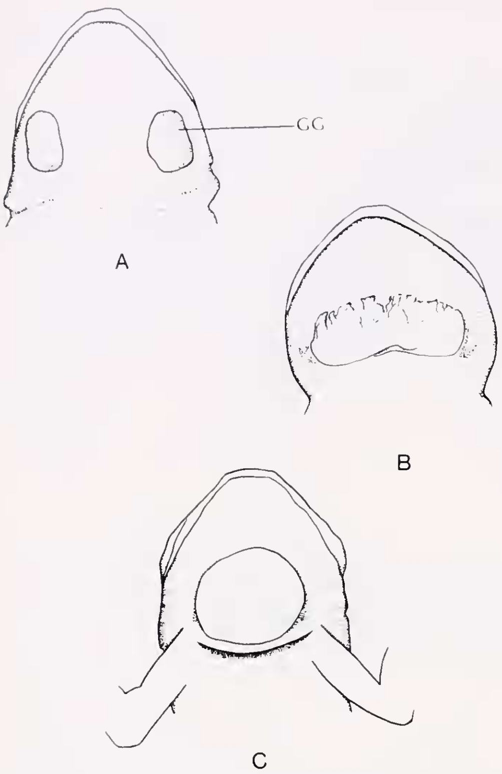

Figure 14. Gular gland/vocal pouch apparati. A) *Acanthixalus spinosus* (MHNG 1033.75), B) *Callixalus pictus* (CAS 104963), and *Opisthothylax immaculatus* (TNHC 38622). Key: GG, gular gland.

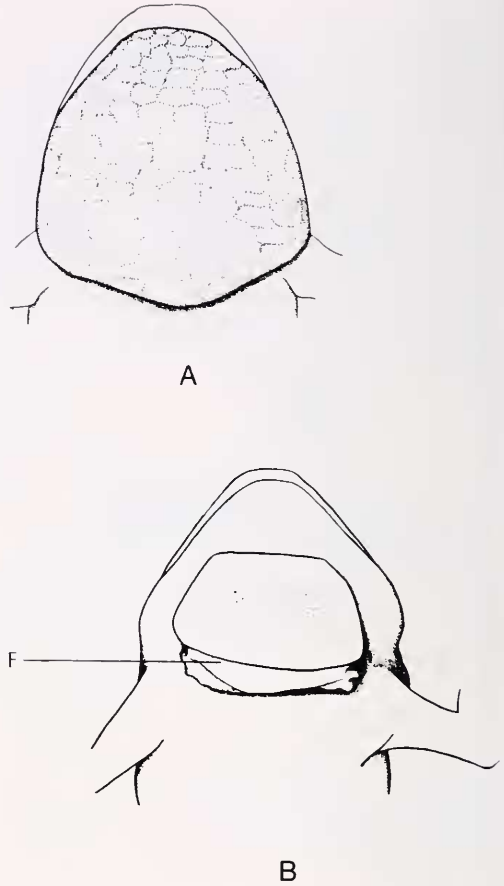

Figure 15. Gular gland/vocal pouch apparati. A) *Cryptothylax gresshoffi* (CAS 145277), B) *Hyperolius argus* (CAS 148505). Key: F, loose folds of non-distensible skin underlying gland.

present, located near the articulation of jaws; vocal pouch absent (Fig. 14A)

State 2. Gular gland anteromedially reduced to an indented, transverse oval; vocal pouch absent (Fig. 14B)

State 3. Gular gland a median disc or oval surrounded by loose, thin, unfolded, nondistensible skin (vocal pouch; Fig. 14C)

State 4. Gular gland greatly enlarged so that it obscures entire gular region and even overlaps ventral margins of lower jaw; vocal pouch absent (Fig. 15A)

State 5. Gular gland a median disc, oval or rhomboid; the lateral and posterior margins free and overlie vocal pouch, which consists of extensive folds of thin, nonpleated skin (Fig. 15B)

State 6. Gular gland a small thick disc, the lateral and posterior margins of which are well defined and more or less free. Gland overlies thick, lateral and posterior densely pigmented skin (generally hidden in living specimens); vocal pouch consists of thick, pleated, elastic skin that extends caudally to include part of pectoral region (Fig. 16A and see character 21)

State 7. As in state 6, except gular gland straplike, with only lateral margins well defined and free. (In *K. maculata*, posterior margin of gular gland free, but pigmented skin confined to beneath lateral portions of gland) (Fig. 16B)

Direction of change. Leptopelis is the only hyperoliid genus whose members lack both vocal pouch and gular gland (state 0). Liem (1970) considered this character state to be primitive because it exists in the ranids he examined. The same is true for all of the outgroup species examined here. Furthermore, *Leptopelis* exhibits the primitive state of a large number of characters, and thus by outgroup comparison and character correlation, state 0 is considered primitive (criteria 1 and 2).

State 3 is considered the earliest derivative from state 0 because it is the simplest in structure, and it is present in forms that possess primitive or intermediate states of other characters (character correlation). State 4 is unique to *Cryptothylax,* and apparently derived from state 3. Three additional lineages are apparently derived from state 3. State 5 represents an elaboration of the same thin, nondistensible skin, present in state 3, into a more distensible vocal pouch; states 6 and 7 are more complex and made up of integumental structures quite dissimilar to those of states 3 and 5. States 2 and 1 would seem to represent a trend toward reduction of the gular gland. The directions of change for this character can be visualized as follows:

$$\begin{tikzcd}
 & 1 & & \\
 & 2 \arrow[u] & & \\
0 \arrow[r] & 3 \arrow[r] \arrow[u] \arrow[d] \arrow[dr] & 6 \arrow[r] & 7 \\
 & 4 & 5 &
\end{tikzcd}$$

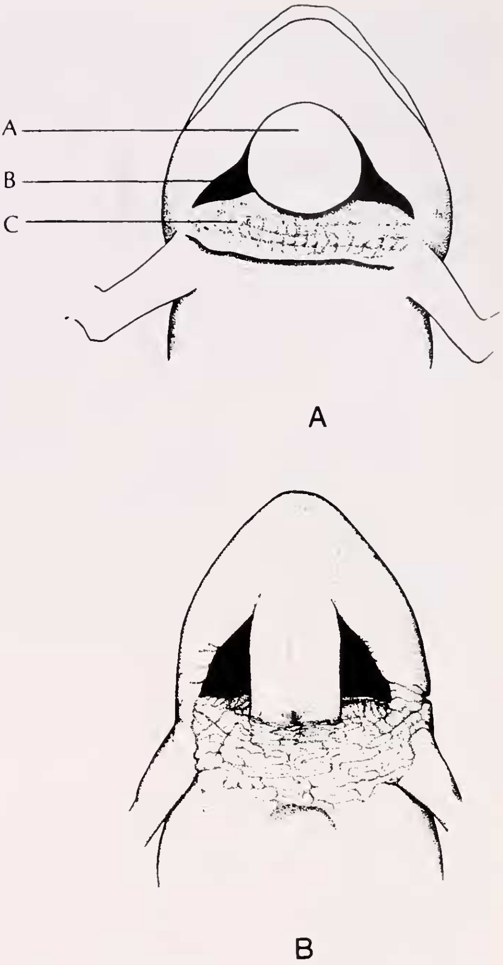

FIGURE 16. Gular gland/vocal pouch apparati. A) *Phlyctimantis leonardi* (CAS 141781), B) *Kassina senegalensis* (CAS 146411). Key: A, gular gland; B, densely pigmented skin of accessory pouches underlying gland; C, thick, pleated, distensible tissue of vocal pouch. Note posterior extent of pleated tissue in B.

19. Vocal sac openings, nature of. Liu (1935) surveyed and described the types of vocal sacs and vocal sac openings in 559 species of anurans. Liu followed Boulenger (1896), Gadow (1909), and Noble (1931) in describing vocal sac apertures simply as round or slit openings, although he disagreed with the first two workers on certain specific observations. That frogs call with the mouth and nares tightly closed (Liu 1935; Noble 1931; Schmidt 1965; and many others), suggests that the vocal sac openings are passive and the entire call mechanism is a closed system. However, Gans (1973, 1974) observed that rising buccal pressure does not by itself inflate the vocal sac, and he considered the vocal sac openings "independently operated, valvular" closures.

Many frogs keep the vocal sac inflated after calling, and my own field and laboratory observations on hyperoliids (especially *Kassina*), suggest that members of some species can maintain a fully inflated vocal sac for at least one minute after calling (and probably longer). Wager (1965) observed this phenomenon in *Kassina wealei.* In these examples, it seems unreasonable to assume that the vocal sac apertures are passive; otherwise, the frog would not be able to respire while maintaining a fully inflated vocal sac.

Careful dissection of gular regions suggests that some species of hyperoliid frogs have vocal sac openings that are sphincters, whereas others possess openings that are slitlike and partially supported by cartilage of the hyoid, as are those in the Hylidae described by Tyler (1971). The

FIGURE 17. Frontal section of sphincter vocal sac opening of *Leptopelis christyi* (CAS 111641). Note lining of lumen (center of section), which is continuous with the lining of buccal cavity. Section made at 10 microns and stained with Hematoxylin/Eosin, by Department of Anatomy, Stanford University School of Medicine.

mechanism of closure of the latter structures is unknown. Serial frontal sections of *Leptopelis viridis, L. christyi,* and *Philautis acutirostris* reveal that the apertures are sphincters composed of anastomotic skeletal muscle (most probably the m. petrohyoideus anterior [M. J. Tyler, Univ. Adelaide, pers. comm.]), reminiscent of the transitional muscle found in vertebrate digestive tracts (M. R. Miller, UCSF, pers. comm.). Furthermore, there is an admixture of muscle fibres suggestive of a sphincter (M. J. Tyler, pers. comm.; Fig. 17). The inner lining of these sphincters appears to be mucosal tissue continuous with that of the buccal cavity. To my knowledge, the only other investigator to have observed the true nature of these vocal sac openings is Jean-Luc Perret (1966).

Apparently, the two types of openings are derived independently, and are thus treated separately. The species lacking a vocal sac opening of any kind are included in character 20 as they possess developments of the anterior horn of the ceratohyal similar to the rest of the hyperoliids, all of which have slitlike vocal sac openings.

Two states of sphincteral vocal sac openings are recognized:

State 0. Vocal sac openings are posterior sphincters located near articulation of jaws and within an area created by the medial bowing of the ceratohyals. Apertures supported by discrete bundles of m. petrohyoideus anterior; a posterior slip originates near angle of jaws, lateral slips attach to mandibles and ceratohyals, and anterior slips course forward and then bend medially to insert on anterior process of ceratohyal, beneath the m. geniohyoideus medialis (Figs. 5C, 18)

State 1. Vocal sac openings not sphincters

Direction of change. Sphincteral vocal sac openings are present in most of the ranines, astylosternines, and arthroleptines studied (also see Perret 1966). In fact, the sphincters in *Leptopelis* are remarkably similar to those of *Hylarana*, including the supportive medial bowing of the ceratohyals. The main difference between the two

FIGURE 18. Ventral photograph of sphincteral vocal sac opening *in situ* in *Leptopelis karissimbensis* (CAS-SU 13019). Opening is visible (lower arrow), medial bowing of ceratohyal is apparent (middle arrow) as are fibres of m. petrohyoideus anterior coursing anteriorly (upper arrow) (refer to Fig. 5C, drawn from this specimen). Photo by John E. Simmons (CAS).

is that in *Hylarana* the sphincters are contained within the ceratohyal space—no anterior slips of m. petrohyoideus anterior insert on the anterior process of the ceratohyal. The process is free, uninvolved in muscle attachment. Therefore, sphincters (state 0) are considered primitive by outgroup comparison, and the direction of change can be visualized as:

$$0 \rightarrow 1$$

20. Vocal sac openings, position of. In all hyperoliids possessing vocal sac openings, they are slitlike, except in *Leptopelis*. These structures are formed by modifications of the epithelial lining of the mouth and are not muscular. In every case, their medial margins are formed by the ceratohyals. The vocal sac openings lie dorsal to the ceratohyals and appear to collapse upon them when shut. A group trend among hyperoliids appears to be the migration of the vocal sac opening from a posterior position to an anterior one (most common). Four states for position of vocal sac opening are recognized for the Hyperoliidae:

State 0. Vocal sac openings are posterior sphincters; (state 0, character 19)
State 1. Vocal sac openings are lateral (slits), located beneath eye; medial margins of apertures formed by ceratohyals (Fig. 5A)
State 2. Vocal sac openings are anterior (slits) posteromedial borders formed by anterolateral margins of lateral processes of anterior horn of hyoid (Fig. 5B)
State 3. Vocal sac openings absent

Direction of change. Among the comparative material examined, only the Phrynobatrachinae and *Hemisus* possess slitlike vocal sac openings: both reflect state 1. Most hyperoliids studied exhibited state 2. State 1 is considered a transitional state in the direction toward evolution of anterior slitlike vocal sac openings. Possession of states 1 and 2 is correlated with possession of other primitive and transitional character states. State 3 may be derived from either states 1 or 2. Thus, by outgroup comparison and character correlation, the direction of change is:

$$\begin{tikzcd}
0 \arrow[r] & 1 \arrow[rr] \arrow[dr, dotted] & & 2 \arrow[dl, dotted] \\
& & 3 &
\end{tikzcd}$$

21. Vocal sac musculature. Since Liu's survey in 1935, the superficial mandibular musculature that makes up the vocal sacs of male anurans has been rarely treated as a systematic character. In 1971, Tyler published three papers on the vocal sac apparatus and associated structures. In the first (1971a), he discussed the phylogenetic significance of the vocal sac and resurrected the genus *Litoria* for Australo-Papuan frogs formerly of the genus *Hyla*. In the second (1971b), he described various myo-integumental attachments associated with the vocal sac, including septa of the mandibular, pectoral and abdominal lymph sacs (recently treated in more detail by Carter [1979]), and the m. cutaneous pectoris, a myo-integumental muscle of the pectoral region. In the third (1971c), he treated the m. cutaneous pectoris as a taxonomic character, having found it exclusively among the Ranidae (*sensu lato*, including the rhacophorids and hyperoliids).

The anuran vocal sac is composed of various modifications of the m. interhyoideus of the hyoid muscle complex, which when inflated becomes a resonating chamber. Typically, the m. interhyoideus originates on the crista parotica of the skull near the termination of the ceratohyal of the hyoid. The muscle follows the ceratohyal ventrally to the postarticular portion of the mandible. At this point, the anterior horn passes anteriorly while the interhyoideus diverges medially to form a transverse panniculus. The interhyoideus is united with the m. intermandibularis anteriorly and is posteriorly connected by a sheet of connective tissue to the m. episternohumeralis (Tyler 1971a). The site of the pectoral septum, which separates the pectoral lymph sac from the abdominal lymph sac, apparently marks the posterior boundary of the inflated vocal sac (Tyler 1971b). Externally, this boundary is often visible in ventral view as a pectoral fold, or in some species of *Kassina*, and in *Phlyctimantis*, *Tornierella*, and *Kassinula*, as the posterior extent of thick, distensible skin. Many species of *Kassina* possess extremely large vocal sacs. In ventral view, the relaxed vocal sacs of preserved specimens commonly obscure much or all of the pectoral musculature beneath them. In such species, the pectoral septum is steeply slanted, originating along the posterior edge of the m. pectoralis sternalis and inserting on the ventral surface of the ventral skin at about the level of the last inscription of the m. rectus abdominis (Fig. 12).

My field and laboratory observations support Tyler's suggestion (1971c) that the pectoral septum is the interior boundary to posterior expansion of the vocal sac, for in *Kassina parkeri*, *K. senegalensis*, and *K. cochranae*, all of which possess slanted pectoral septa, much or most of the pectoral region is invaded by the inflated vocal pouch (Fig. 12).

Both species of the genus *Tornierella* possess vocal sacs unique among the Hyperoliidae and perhaps among the Anura. In *T. kouniensis*, the origin of the m. interhyoideus has shifted to the dorsal fascia at the midline of the back of the skull just posterior to the frontoparietals. From here, the thick noninflatable slip passes laterally, overlying the origin of the m. adductor mandibulae posterior longus and the anterior third of the m. rhomboideus anterior, then ventrally, deep and medial to the depressor mandibulae musculature. On the inner surface of the retroarticular process of the mandible, the interhyoideus passes through a connective tissue trochlea, then passes anteriorly and finally medially as in the normal condition. Supramandibular development of the interhyoideus is similar in *T. obscura*, but the slip is thinner and the origin variable—either on the middle portion of the dorsal fascia of the m. adductor mandibulae posterior longus or on the otoccipital, just beneath the posterior edge of the a. m. posterior longus. Dissection of several specimens revealed that no other muscle originates from the usual point of origin, which suggests that the shift of origin of the interhyoideus was not caused by displacement.

Supramandibular developments of the interhyoideus have been reported for a number of frogs (Liu 1935; Duellman 1956; Tyler 1971a), but in most frogs (but not *Hyla pulchrilineata* [see Tyler 1971a]) these structures are inflatable and thus part of the resonating apparatus of the vocal pouch. In any event, in these other examples the supramandibular structures are external or posterior to the depressor mandibulae complex, not deep to it.

Eight character states of the vocal sac musculature are recognized:

State 0. Vocal sac absent
State 1. Vocal sac simple, fibers of m. interhyoideus remain parallel (Fig. 19A)
State 2. Vocal sac composed of anterior development of interhyoideus only, so that

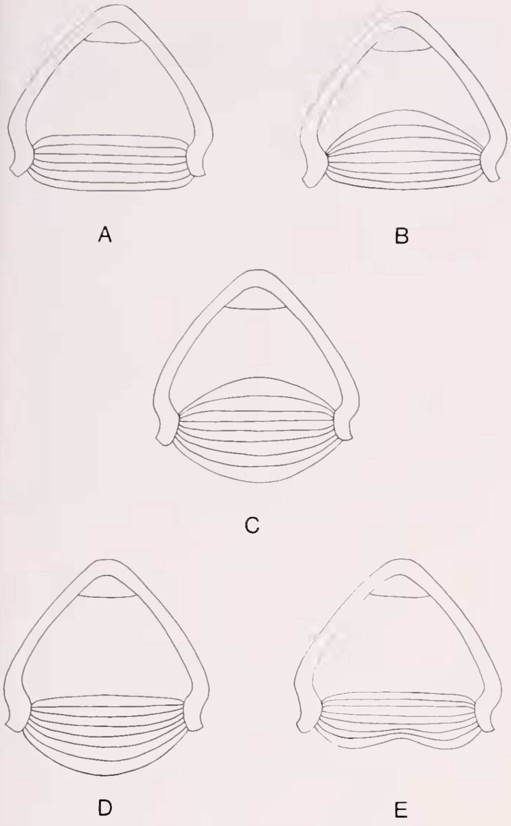

Figure 19. Vocal sac musculature (schematic figures after Tyler 1971a). A) simple vocal sac composed of horizontal fibres of m. interhyoideus, B) vocal sac composed of anterior development of m. interhyoideus at expense of m. intermandibularis, C) both anterior and posterior development of m. interhyoideus, D) posterior development of m. interhyoideus only, E) posterior development into bilobular configuration.

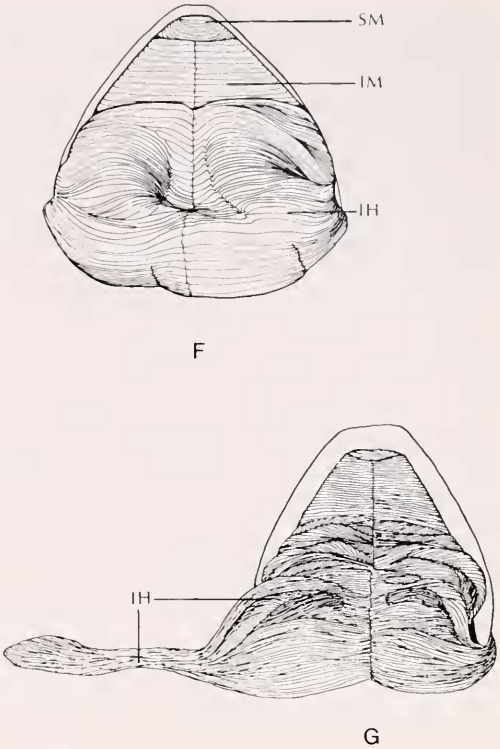

Figure 20. Vocal sac musculature. F) *Kassina senegalensis* (CAS 141663) showing great anterior and posterior development of m. interhyoideus, G) *Tornierella kouniensis* (CAS 145356) showing unique supramandibular development of m. interhyoideus. Key: SM, m. submentalis; IM, m. intermandibularis; AP, accessory pouches of vocal sac; IH, m. interhyoideus. (Drawn by Peggie Phillips.)

it comprises, at the expense of the m. intermandibularis, about ⅓ of superficial mandibular musculature (Fig. 19B)

State 3. Vocal sac composed of posterior development of interhyoideus only; posterior lobe does not extend beyond anterior margin of m. supracoracoideus caudally (Fig. 19D)

State 4. As in state 3, except that vocal sac slightly bilobular (Fig. 19E)

State 5. Vocal sac composed of both anterior and posterior development of interhyoideus, a combination of states 2 and 3 (Fig. 19C)

State 6. As in state 5, but development of vocal sac much more extensive; anteriorly, the interhyoideus makes up more than ⅓ of superficial mandibular musculature, and extends posteriorly at least to posterior margins of m. supracoracoideus. (In some species, all of the pectoral musculature is hidden.) Two midlateral, invaginated pockets underlie densely pigmented lateral portions of gular pouch on either side and beneath gular gland (Figs. 13, 20A and see character 18)

State 7. As in state 6, except origin of interhyoideus shifted, visible laterally as it passes deep to m. depressor mandibulae (Fig. 20B)

Direction of change. Most ranids examined possessed either state 1 or state 3, with the exceptions of *Ptychadena, Dicroglossus, Rana ridibunda,* and *R. cyanophlyctis,* which have bilobular vocal sacs (a more derived condition similar to state 4 above). State 3 is considered the primitive condition by character correlation (criterion 2). State 4 is a slight modification of state 3; species demonstrating state 0 are linked to those possessing state 4 by other derived character states (criterion 2). Species exhibiting states 0 and 4 are apparently part of a separate lineage derived from state 3 by modification of posterior elements of the vocal sac only. State 1 is the simplest configuration, apparently separately derived from state 3. States 2, 5, 6, and 7 represent a lineage of species that have vocal sacs that are increasingly complex and involve modification of the anterior portions of the vocal sac and reduction of the m. intermandibularis. The direction of change is visualized here as:

$$\begin{tikzcd}
1 & 3 \arrow[l] \arrow[r] \arrow[d] & 2 \arrow[r] & 5 \arrow[r] & 6 \arrow[r] & 7 \\
& 4 \arrow[d] & & & & \\
& 0 & & & &
\end{tikzcd}$$

22. Pupil. The shape of the pupil in hyperoliid frogs appears to be constant within genera. Two states of pupil shape are recognized:

State 0. Pupil a horizontal oval or nearly round
State 1. Pupil vertically elliptical or rhomboidal

Direction of change. In most ranoid frogs studied, the shape of the pupil is round or a horizontal oval. Lynch (1973) pointed out that most authors have treated the round pupil as primitive because it is much more common than the vertical pupil but that most archaic and transitional families have vertical pupils. Lynch treated the vertical pupil as the primitive state; I concur and thus the polarity of this character may be visualized as:

$$0 \leftarrow 1$$

23. Tympanum. Peters (1964) defined the tympanum as the "membrane covering the external opening of the middle ear chamber or vestibule" and cautioned that great care must be taken in citing its presence or absence. In many frog species, the tympanum is present and stretched across the annulus tympanicus but completely masked from external view by epidermis. Many workers on hyperoliids have described the condition of the tympanum as indistinct or hidden (Schiøtz 1967, 1975), or "hidden beneath the skin" (Guibé 1978). Lombard and Bolt (1979) cited studies that demonstrated that many such species can detect airborne vibrations almost as well as or as well as species in which the tympanum is external. In most species of the Hyperoliidae, the tympanum is externally exposed and obvious. In certain populations (e.g., *Afrixalus*), however, the tympanum, or portions of it, may or may not be visible from individual to individual. In others (e.g., *Callixalus*) it is always internal and thus externally invisible. Curiously, in the original descriptions of two species of the latter category (both representing monotypic genera), the describer failed to note the absence of an external tympanum (Laurent 1950, 1951). Among the species I examined, I noted three character states:

State 0. Tympanum, or any portion of it, externally visible
State 1. Tympanum visible or hidden; in a given population, some specimens have tympanum or some portions of it visible, in others it is not observable
State 2. Tympanum (including annulus tympanicus) always obscured by epidermis, or absent

Direction of change. Most frogs have externally visible tympani; thus state 0 is considered primitive by outgroup comparison (criterion 1). Some hyperoliid species exhibit individual variation regarding the presence or absence of this character, suggesting a tendency toward loss of the structure within the group as a whole. My observations suggest that this character state is not a preservation artifact. Care must be taken in working with desiccated specimens, in which the epidermis may be drawn tightly against the annulus tympanicus, giving the impression of an externally visible tympanum. The direction of change of this character can be illustrated:

$$0 \rightarrow 1 \rightarrow 2$$

24. Intercalary elements. Intercalary elements are small cartilaginous structures, mineralized or not, that are located between the penultimate and terminal phalanges of several families of arboreal frogs. Intercalary elements have been considered taxonomically significant and in part characterize such families as the Hylidae, Pseudidae, Rhacophoridae, and Hyperoliidae. Early workers such as Peters (1882), Boulenger (1888), Parker (1931, 1935), and Noble and Jaeckle (1928), referred to these structures as "accessory" or "additional phalanges," "intercalary elements," or "intercalary bones"; however, in recent years they have usually been described as "intercalary cartilages" (Duellman 1970; Liem 1970; Goin and Goin 1971; Porter 1972; Dowling and Duellman 1978; Emerson and Diehl 1980).

In addition to hyperoliid material, I examined other species of frogs with intercalary elements. The clearing and differential-staining technique employed revealed that the term "intercalary cartilage" is somewhat misleading. In most adult specimens examined, the intercalary elements, though fundamentally cartilaginous, are either partially or wholly mineralized, staining readily in Alizarin Red S. Very few species have unmineralized, purely cartilaginous intercalaries. Noble and Jaeckle (1928) stated that the intercalary element of *Polypedates leucomystax* is "fully ossified bone with a marrow cavity and cartilaginous articulating surface. It differs in this respect from *Hyla*, where the intercalary is composed of fibrous cartilage." I have only examined the intercalary of *P. leucomystax* externally in cleared and stained specimens, but serial longitudinal sections of the element of *Kassina senegalensis* (Fig. 23), which is of identical shape (see below), reveal that the intercalary element is no more than fully mineralized cartilage. No marrow cavity was found.

The function of intercalary elements is not well understood. Noble and Jaeckle (1928) suggested that the intercalary increased the efficiency of the toe pad apparatus by providing "bony" support to the proximal part of the toe pad. They reported that in individuals of *Hyla* observed slipping off smooth rock, the proximal part of the toe pad remained closely adpressed to the substrate, while the distal portion "makes a series of attempts to secure a better hold." Citing the existence of large numbers of arboreal frogs lacking intercalary elements, and terrestrial forms possessing them, Noble and Jaeckle concluded that intercalary elements, though not essential to arboreal life, usually arose in association with it. They concluded further that all of the other components of the toe pad mechanism had already evolved before the intercalary appeared and are not necessarily associated with arboreal life. It seems apparent that intercalary elements have evolved independently in several groups.

The various shapes of intercalary elements are rarely treated in systematic constructs. Perhaps because they are difficult to examine, they are often given only generalized descriptions in the literature. For instance, the family Hylidae is often said to have "disc-shaped intercalary cartilages" (Duellman 1970). However, examination of the toe tips of several members of that family reveals different configurations. The only disc-shaped intercalaries seen among the hylids I examined were those of *Hyla smithi* (mineralized), *Litoria aurea* (cartilaginous), *Triprion spatulatus* and *L. dahli* (presumably mineralized, see figure in Tyler 1978). In *Agalychnis callidryas,* the intercalary is an enlarged cartilaginous cup with a rounded dorsal eminence that invests the terminal phalanx proximally and may not be separate from it. This structure could be a simple enlargement of the epiphysis of the terminal phalanx and is in need of study. Similar structures were seen in *Hyla arborea, Litoria caerulea,* and *Phrynohyas venulosus.* Intercalary elements are apparently absent in *Pternohyla dentata.* In *Acris gryllus, Pseudacris nigrita, Litoria arfakiana,* and *L. becki,* the intercalaries are wedge shaped as in the hyperoliids (see below).

The shapes of intercalary elements vary among other groups as well. In the pseudids *Pseudis paradoxus* and *Lysapsus limellus,* the intercalaries are elongate and very similar to normal phalanges (see Savage and Carvalho 1953). Among the Rhacophoridae, *Philautis acutirostris* has disclike intercalaries, whereas *Polypedates leucomystax, Chiromantis petersi, Mantidactylus ulcerosus, Philautis variabilis* and *P. lissobrachius* have wedge-shaped elements like those of the hyperoliids. The intercalaries of the microhyloid *Phrynomerus bifasciatus* are strongly concave, thick discs.

Except for members of the genus *Leptopelis* (treated below), the intercalary elements of corresponding fingers of individuals of different hyperoliids are invariably the same shape, although they may differ in size from species to species. This suggests that the structures are homologous within the family Hyperoliidae.

The intercalary element of the third finger is described here. Among hyperoliids, it is fairly

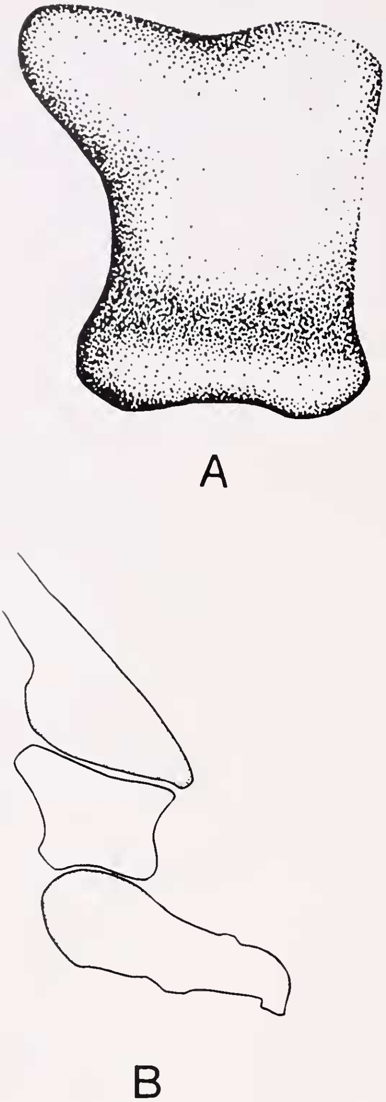

Figure 21. Intercalary elements. A) detailed right lateral view of intercalary element of third finger of *Kassina parkeri* (CAS 140352). B) lateral view of intercalary element of third finger of *Acanthixalus spinosus in situ* (BM 1938.1.11.22). In B) stippled areas indicate cartilaginous epiphyses of penultimate and terminal phalanges.

large compared with the "discs" of some of the non-hyperoliid species; it is generally at least 50% of the length of the terminal phalanx (Fig. 15B). It is wedge shaped, rounded anteriorly and slightly concave posteriorly. The distal end is sharply concave where it articulates with the medial rounded portion of the terminal phalanx. The dorsal articular surface is slightly concave and bears a proximal flange that extends posteriorly to about the posterior limit of the epiphysis of the penultimate phalanx (Fig. 21A). *In situ*, the intercalary element is slightly inset so that dorsally a portion of the epiphysis of the penultimate phalanx overhangs its proximal end (Fig. 21B). The width of the proximal end of the intercalary is less than that of the proximal phalanx, but distally it widens to equal to it.

Intercalary elements are completely mineralized in adult specimens of 7 of the 14 hyperoliid genera recognized here: *Acanthixalus, Chrysobatrachus, Cryptothylax, Kassina, Opisthothylax, Phlyctimantis* and *Tornierella*. Juvenile specimens are scarce, but at least in postmetamorphic examples of *Kassina senegalensis* and in the rhacophorid *Chiromantis petersi*, the intercalary elements are cartilaginous and not yet mineralized. Mineralization is apparently perichondral as shown by staining densities in serial sections. Also, in four genera that have partially mineralized intercalaries as adults—*Afrixalus, Callixalus, Hyperolius* and *Heterixalus*—mineralization is readily seen to be peripheral in cleared and double-stained individuals, the central portion of the element remaining cartilaginous (Fig. 22, right). Two additional genera, *Tachycnemis* and *Kassinula*, retain cartilaginous intercalary elements as adults, but these are the same shape as in the others.

The intercalary elements of members of the genus *Leptopelis* are unique among the Hyperoliidae. The intercalaries of all the *Leptopelis* I examined (Appendix A) failed to accept either Alizarin Red S or Alcian Blue stain, although other cartilaginous structures in the same specimens stained normally. Under magnification, the intercalaries of cleared specimens are barely visible as transparent amorphous masses with indistinct outlines (Fig. 22, left). Only one specimen, *L. hyloides* (CAS 141772), showed evidence of slight mineralization, and then asymmetrically in three elements of one foot and one of the other. The mineralization is unlike the perichondral mineralization of *Afrixalus, Hyperolius*, or *Heterixalus* (Fig. 22, right). Serial longitudinal sections of the third toe tip of *L. karissimbensis* (CAS 98211) were made and compared with similar sections of *Kassina senegalensis* (Figs. 23, 24). The *Leptopelis* interca-

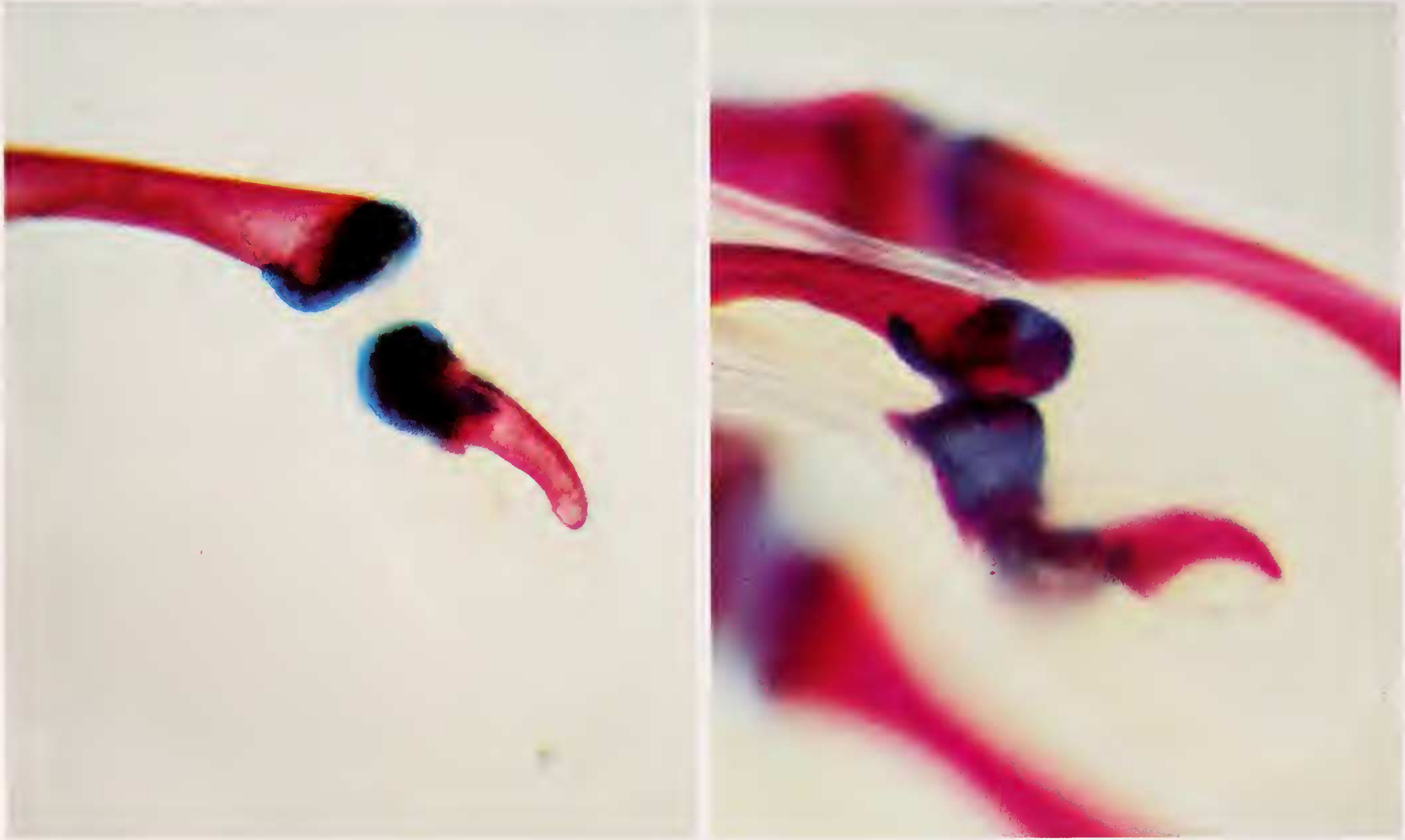

FIGURE 22. Left: Photograph of cleared and double-stained third toe tip of *Leptopelis bocagei* (CAS 141455). Red is bony, blue is cartilaginous. Note that while the epiphysis of the penultimate phalanx accepts blue stain, the intercalary element does not; it is barely visible.

Right: Photograph of cleared and double-stained toe tips of an adult *Afrixalus fornasinii* (CAS 135862). Note that the intercalary element is perichondrally mineralized; the center of the element remains cartilaginous (blue).

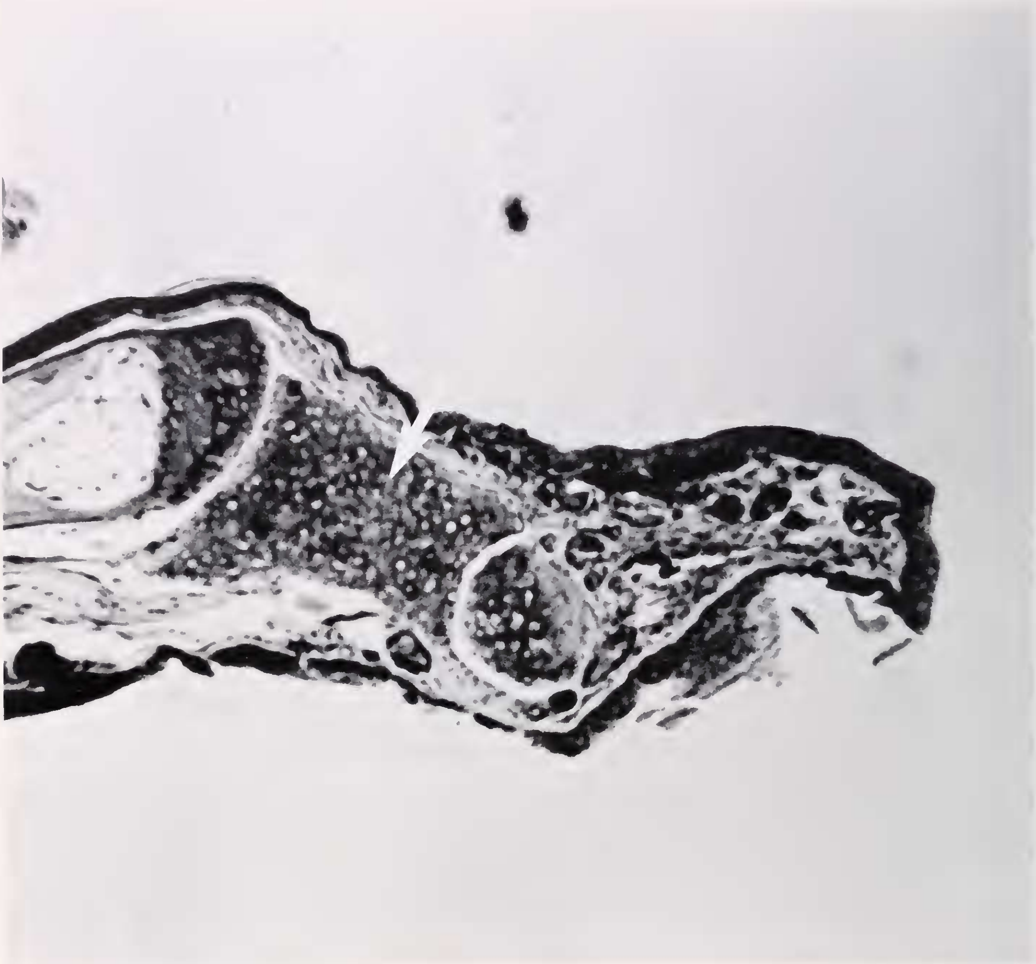

FIGURE 23. Sagittal section of toe tip apparatus of adult *Kassina senegalensis* (CAS 143398). Note the intercalary element at center stains darkly (arrow), as does the epiphysis of the penultimate phalanx—a cartilaginous matrix is present. Section was made at 10 microns and stained in Hematoxylin/Eosin by Dr. Ben Lung, University of Colorado Medical School.

lary resembles that of *Kassina* in shape and position—the proximal flange is present, and the distal articular surface is concave. The histology, however, is strikingly different. In *Leptopelis*, the element is composed of closely packed chondrocytes, virtually devoid of intracellular matrix. Drs. Malcolm R. Miller and C. Willet Aslin of the University of California, San Francisco, concluded that the elements are hyaline cartilage in a juvenile state.

Leptopelis is unquestionably a basically arboreal group (Schiøtz 1967, 1975) with the exceptions of *L. bufonoides*, *L. bocagei*, and possibly *L. viridis*. The first two species are fossorial; the third is often found beneath compost heaps (T. J. Papenfuss, University of California, Berkeley, pers. comm.). *Leptopelis bocagei* and *L. viridis*, included in the present study, are histologically like the arboreal *L. brevirostris*, *L. boulengeri*, *L. christyi*, *L. hyloides*, *L. karissimbensis*, *L. kivuensis*, *L. macrotis*, *L. modestus*, and *L. notatus*.

Four states of this character were observed among the Hyperoliidae:

State 0. Intercalary elements of adult frogs are juvenile cartilage; no intracellular matrix formed (Figs. 22, left; 24)

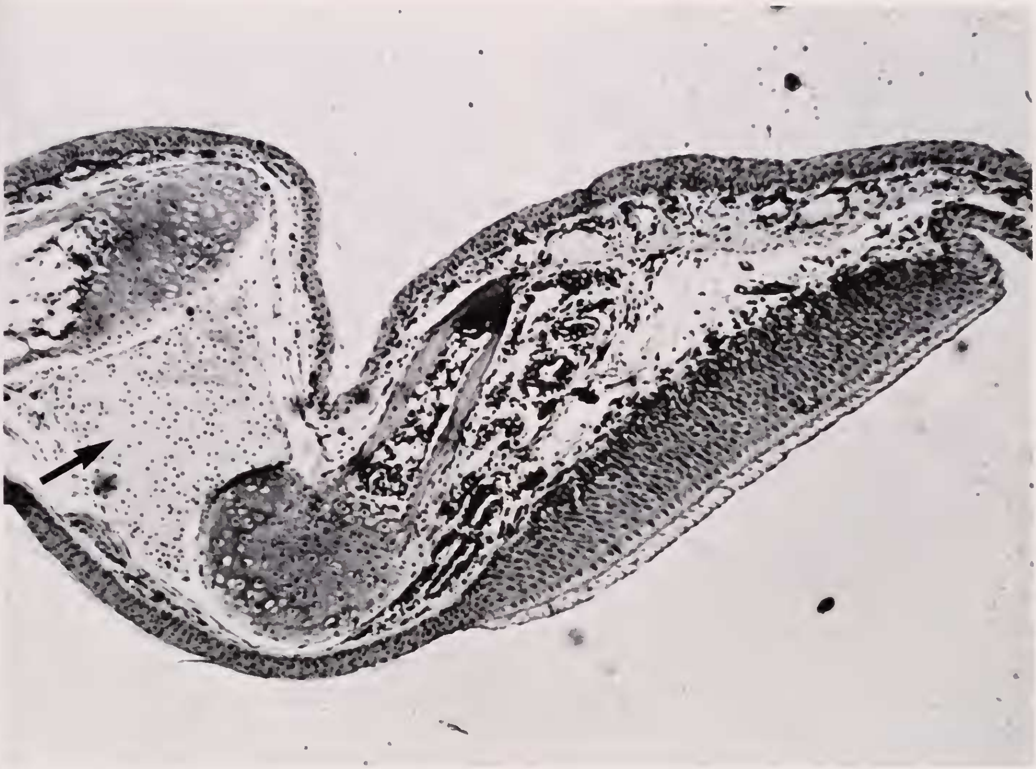

FIGURE 24. Sagittal section of toe tip apparatus of adult *Leptopelis karissimbensis* (CAS 98211). Note that the intercalary element (arrow) does not stain darkly as do the epiphyses of the penultimate and terminal phalanges—no intracellular matrix is present. The cartilage is juvenile. Section was prepared by Ben Lung, as that in Fig. 23.

State 1. Intercalaries of adult frogs cartilaginous, unmineralized
State 2. Intercalaries of adult frogs peripherally mineralized, central parts of elements remain cartilaginous (Fig. 22, right)
State 3. Intercalaries of adult frogs completely mineralized (Figs. 9, 23)

Direction of change. I consider the intercalary element a low-weight, highly variable character. Direction of change can be visualized in two different ways. If state 3 is considered primitive based on character correlation, then the direction of change can be represented as follows:

$$\begin{tikzcd} 3 \arrow[r] \arrow[d] \arrow[dr] & 2 \\ 0 & 1 \end{tikzcd}$$

This holds true only where states 0, 1, and 2 have evolved several times by reduction. If state 0 is considered primitive, a relictual precursor, then the direction of change can be represented as:

$$\begin{tikzcd} 0 \arrow[r] & 3 \arrow[r] \arrow[dr] & 2 \\ & & 1 \end{tikzcd}$$

In this analysis, the latter alternative was chosen. Both options were employed, however, and both result in the same cladogram.

25. *Metasternum.* All Hyperoliidae and the arthroleptine and astylosternine ranids possess flat, cartilaginous metasterna. In other Ranoidea, the proximal part of the sternal elements is fully ossified into a bony style, the distalmost portion remaining cartilaginous. This character and the three that follow have been coded for the purposes of assessing familial relationships (see Fig. 11). I recognize two character states among the ranoids studied here:

State 0. The metasternum is cartilaginous

State 1. The metasternum includes a bony style

Direction of change. The cartilaginous metasternum is considered primitive as it is not only present in members of the Archeobatrachia (Leiopelmatidae, Discoglossidae, Pipidae, and Pelobatidae) but scattered among many neobatrachian groups such as the leptodactylids, bufonids, brachycephalids, pseudids, hylids, sooglossids, microhylids and some ranids (outgroup comparison, criterion 1). The direction of change may be illustrated as:

$$0 \rightarrow 1$$

26 & 27. Carpal and tarsal fusion. Howes and Ridewood (1888), Steiner (1921), Stephenson (1952), Laurent (1940, 1941, 1942a), Ritland (1955), and Jarošová (1973, 1974) have described the carpals and tarsals in a number of frog species. Liem (1970) utilized carpals and tarsals in his analysis of the Old World treefrogs.

When the element just proximal to the prepollex is considered the first carpal (Steiner 1921), one of two conditions may be found: either the first, second, and third carpals and the first centrale are free, and the fourth and fifth carpals are fused with the second centrale (the "free third carpal" of Laurent 1940, 1941, 1942a), or the third carpal is also fused with the second centrale. The first condition is usually considered primitive, as it has been found in discoglossids (Howes and Ridewood 1888; Jarošová 1973) and leiopelmatids (Stephenson 1952; Ritland 1955), whereas in most advanced frogs, the third carpal and centrale are fused (Howes and Ridewood 1888; Liem 1970).

A similar trend involving fusion is found in the tarsals of advanced frogs (Noble 1931). The Discoglossidae, Leiopelmatidae, and *Pelodytes* exhibit the primitive state; i.e., the second and third tarsals are free (Howes and Ridewood 1888; Stephenson 1952; Ritland 1955; Jarošová 1974). In more advanced forms, the second and third tarsalia are fused (the os cuboideum), leaving only the first free if it is present. With respect to identification of the individual tarsalia, Liem (1970) was incorrect in his text and figures. Howes and Ridewood (1888) demonstrated that the os cuboideum was the result of the fusion of the second and third tarsals, not the second, third, and fourth. They also showed that the element at the base of the prehallux that Liem figured (1970; Figs. 44, 45) as the first tarsal is actually the naviculare, a centrale which is the point of insertion for a tendon of the m. adductor longus digiti primi. The first tarsal (hallux-tarsal) is not always present. When present it can be overlain by the naviculare or sandwiched between it and the first metacarpal laterally.

The carpalia of all hyperoliids I examined were unfused, and the third carpal was free, as were the second and third tarsals. These findings are in agreement with those of Liem (1970) for the hyperoliids he examined.

Laurent (1940, 1941, 1942a) described Arthroleptinae and some astylosternine ranids (*Astylosternus, Trichobatrachus*) as having free third carpals, and suggested a relationship with the hyperoliids in part on this basis. Poynton (1964) disagreed, stating that the arthroleptines demonstrated the fused carpal condition. In a much later paper, Laurent (1973) reiterated that the Arthroleptinae were characterized by the free third carpal except in "some forms of *Schoutedenella* where it is fused with the second carpal and first central. There is a possibility that this fusion is general in adult specimens of the genus." All of the ranid species I examined had the fused condition, including species of the Arthroleptinae and Astylosterninae, thus confirming Poynton's observations.

Liem (1970) found fusion of carpals and tarsals to be common among the Rhacophoridae, except for *Philautus hosei, Boophis tephraeomystax, Mantidactylus ulcerosus, M. albofrenatus, M. luteus,* and *M. madagascariensis.* In the first two species, he found that the carpals were fused while the tarsals were unfused; in the other four species, he found the reverse to be the case. None of the ranids examined here conforms to this latter configuration—the third carpal is not free in any of the species. There are only two observable states of this character—the carpals are either fused or unfused. Initially the states were coded as:

State 0. Carpals unfused
State 1. Carpals fused

Attempts to derive a relationship between the Hyperoliidae and other ranoids based in part on this polarity were unsuccessful. In light of the highly derived nature of the Hyperoliidae (character correlation) it seemed unlikely that the unfused condition of the carpalia and tarsalia represented retention of primitive characteristics, especially since these conditions are shared only by extant anuran groups phylogenetically remote from the Ranoidea (Discoglossidae, Leiopelmatidae, Pipidae). Therefore, I consider the unfused carpals and tarsals the result of paedomorphic processes and thus derived. For assessment of familial relationships (Fig. 27), the condition of the carpala is labelled character 26 and three character states are assumed for ranoid frogs:

State 0. Carpals unfused (presumed ancestral state)
State 1. Carpals fused
State 2. Carpals unfused, paedomorphic

Direction of change. The direction of change may be illustrated as:

0 → 1 → 2

In all of the ranids examined, the second and third tarsals are fused; in the Hyperoliidae they are free. The condition of the tarsalia is labelled character 27 and coded in an identical manner and on the same basis as the carpalia (see above, character 26). Three character states are recognized for ranoid frogs:

State 0. Tarsals unfused (presumed ancestral state)
State 1. Tarsals fused
State 2. Tarsals unfused, paedomorphic

Direction of change. The polarity of this character may be illustrated as:

0 → 1 → 2

The condition of the first tarsal (hallux-tarsal of Howes and Ridewood 1888) appears to be less conservative among the Ranidae than the condition of the second and third, and may prove to be of taxonomic value. In a number of species the first tarsal is present as a cartilaginous or ossified element. If fusion of tarsalia is a general trend among ranids, retention of the first tarsal must be regarded as primitive. I have not attempted to distinguish between fusion of this element and loss of it. Among the Phrynobatrachinae, the first tarsal is observable only in *Arthroleptella lightfooti* and *Cacosternum boettgeri*; in the remaining species examined, it is apparently either absent or fused. *Hemisus* exhibits the primitive condition (the hallux-tarsal is present), as do all of the astylosternines and arthroleptines examined. In the ranines the distribution of this character is provocative. The first tarsal is absent or fused in *Abrana floweri, Aubria subsigillata, Hylarana, Tomopterna,* and *Pyxicephalus.* The element is conspicuous in *Strongylopus, Ptychadena* and African members of the genus *Rana,* i.e., *R. amieti, R. ruwenzorica, R. angolensis, R. fuscigula,* and *R. desaegeri.* In non-African Old World *Rana,* it is observable but minute in *R. ridibunda, R. temporaria* (Howes and Ridewood found it cartilaginous in this species), and *R. cyanophlyctis.* Among New World *Rana* examined, it is free only in *R. pipiens*; the structure is absent or fused in *R. sylvatica, R. aurora* and *R. palmipes.*

If the above analysis of tarsalia is correct, and fusion or loss of the first tarsal is an evolutionary trend among the Ranidae (most likely via fusion with the naviculare according to Howes and Ridewood 1888), then African *Rana* are the most primitive of the genus with respect to this character, with Old World forms in an intermediate position, and New World forms most derived. Retention of the first tarsal would also place the Arthroleptinae, Astylosterninae, *Hemisus, Ptychadena,* and *Strongylopus* in a primitive position relative to the Phrynobatrachinae, other ranines noted above, and non-African ranids examined.

28. Pectoral musculature. The pectoral musculature of the hyperoliid species revealed a character, first surveyed by Tyler (1971c), that may be of some significance.

The m. cutaneous pectoris is most often a thin rectangular sheet that originates on the abdominal musculature (usually at the level of the last inscription of the m. rectus abdominis and attaches laterally to the m. pectoralis abdominis, medially to the m. pectoralis sternalis) passes anteriorly, and inserts on the deep surface of the ventral integument just posterior to the septum of the pectoral lymph sac (see figures in Tyler 1971b). In some species, the muscle is reduced to a thin slip, but it is still firmly attached to the ventral skin and can be readily observed. The function of the muscle is unknown, although Tyler (1971b) suggested that it may either prevent the separation of tissues or counteract the elasticity of the vocal pouch, thus limiting expansion. Jane Peterson (University of California, Los Angeles, pers. comm.) suggested that the muscle functions in vocalization by male frogs. Contraction of the muscle may pull the pectoral septum in a posterior direction, increasing the size of the pectoral lymph sac (the cavity within which the vocal sac apparatus expands when inflated) and thereby increasing the volume of the resonating chamber. This seems unlikely, as the muscle inserts on the ventral skin, not on the septum itself, although Tyler (1971c) found that in two species the muscle actually perforates the septum and inserts anterior to it. Otto M. Sokol (University of South Alabama, pers. comm.) suspects a possible function in water uptake through the verrucae hydrophilicae of the ventral patch present in some treefrogs (Drewes et al. 1977).

Tyler examined 383 species of 91 genera in 14 families and found the muscle present exclusively in the Ranidae (*sensu lato,* including the rhacophorids and hyperoliids), with the exception of the African genus *Arthroleptis* (three specimens of *A. stenodactylus*). Its presence throughout the ranid-rhacophorid-hyperoliid line emphasized to Tyler the conservative nature of the muscle, and he considered it to have considerable taxonomic significance. Tyler's list of studied material reveals that he examined only two genera presently recognized as members of the Hyperoliidae, *Hyperolius* and *Leptopelis* (*fide* Liem 1970). He examined five specimens of *H. marmoratus* and two of *L. concolor* and found the muscle present in both species, although reduced to a very slender slip (Tyler 1971c).

I have confirmed the presence of the muscle in all of the rhacophorid and most of the ranid genera that I examined (see Appendix A) and that appear in Tyler's list, but I did not find the muscle in any of the hyperoliids, including representatives of the species Tyler examined. Furthermore, the muscle is absent in the following hyperoliids (number of specimens examined given in parentheses): *Leptopelis argenteus* (1), *L. calcaratus* (2), *L. natalensis* (1), *L. rufus* (4), *L. vermiculatus* (1 juv.), *Hyperolius angolensis quarrei* (1), *H. c. cinnamomeoventris* (3), *H. chrysogaster* (2), *H. cystocandicans* (4), *H. frontalis* (2), *H. horstocki* (2), *H. lateralis* (1), *H. marmoratus argentovittis* (2), *H. mitchelli* (1), *H. ocellatus purpurescens* (2), *H. puncticulatus* (1), *H. spinigularis* (1), and *H. sylvaticus* (1).

The muscle is present in the following additional species of the Rhacophoridae: *Buergeria buergeri* (3), *B. japonicus* (4), *Boophis bicalcaratus* (1), *Chiromantis petersi* (2), *C. rufescens* (3), *Mantidactylus ulcerosus* (3), *Micrixalus fuscus* (2), *Philautus acutirostris* (4), *P. glandulosus* (2), *P. longicrus* (4), and *P. schmackeri* (5).

Of additional note are the African Ranidae in which the m. cutaneous pectoris is absent. As might be predicted from Tyler (1971c), it is absent in all of the species of *Arthroleptis* I examined, and also in allied forms, including *Schoutedenella pyrrhocelis, S. hematogaster, S. lameerei muta,* and *Cardioglossa gratiosa.* The muscle is also absent in *Hemisus marmoratum, Astylosternus batesi* and *A. montanus, Arthroleptella lightfooti,* and *A. hewitti,* and *Trichobatrachus robustus.*

Although the m. cutaneous pectoris is but a single character of uncertain function, the results of this study, augmented by Tyler (1971b, c), would seem to support the view that it is conservative in nature (516 species of 124 genera have now been examined) and of considerable taxonomic value.

Two states of the m. cutaneous pectoris are recognized among ranoid frogs:

State 0. The m. cutaneous pectoris is absent
State 1. The m. cutaneous pectoris is present

Direction of change. The presence of the m. cutaneous pectoris is unique to the ranine and phrynobatrachine ranids and rhacophorids studied; it is absent in hyperoliids and astylosternine and arthroleptine ranids. The direction of change is presumed to be:

$$0 \rightarrow 1$$

The following characters were studied but were neither coded nor included in the cladistic analysis. They appear in the generic treatments.

29. Juxtaposition of occipital condyles and cervical cotylar surfaces. Lynch (1971, 1973) described and illustrated three classes of cotylar arrangements that supposedly reflect the degree of lateral displacement of occipital condyles: Type I, the cotyles displaced laterally (widely separated), cup-shaped, sometimes borne on stalks; Type II, the cotyles juxtaposed but distinctly separated, at least by an inter-cotylar groove; and Type III, the cotyles confluent, forming a single articular surface. He considered this a first-degree character, i.e., having the highest degree of confidence, and found it useful as a primary tool in the systematics of leptodactylid frogs. He suggested that the direction of change is from closely juxtaposed to widely separated occipital condyles, because the former state exists in most genera of primitive and transitional frog groups. Type III was considered to be derived from Type II as it was only known from ascaphids and ceratophryine leptodactylids (Trueb 1973).

Clarke (1981) demonstrated that the majority of African ranines show the Type II configuration, finding the Type I arrangement only in *Ptychadena*, and Type III only in the "*Euphlyctis*" group—*Rana tigerina* and *Dicroglossus occipitalis*. Clarke added two species to the Type III configuration, and his findings are in general accord with the conclusions of Lynch with regard to the taxonomic value of this character.

All of the hyperoliid species included in this study have the widely spaced, Type I condylar-cotylar configuration. In four species (*Phrynobatrachus acutirostris, Kassina cassinoides, K. parkeri,* and *K. lamottei*), the cotylar surfaces seem to approach the Type II condition in that they are enlarged and not cup-shaped, but rather ovoid—their ventral margins are deflected somewhat medially. However, in each the surfaces are widely separated (the intercotylar space larger than the diameter of the cotylar surface), and the intercotylar groove is absent. The lack of variation in this character among the hyperoliid material suggests that these species form a natural assemblage.

Most ranid species studied for comparison (those listed under C&S or SKL in App. A) possess either the Type I or Type II arrangement, including *Rana cyanophlyctis*. Type III was observed only in *Rana palmipes*; two subadults show Type II condyles but Type III cotyles, findings similar to those of Clarke in *Dicroglossus occipitalis*. All examples of the subfamilies Raninae and Astylosterninae show Type II configurations. The arthroleptines and *Hemisus* (Hemisinae) have widely spaced condyles—Type I, as do all examples of the Phrynobatrachinae.

30. Configuration of m. depressor mandibulae. The m. depressor mandibulae was examined in a number of frog groups by Griffiths (1954, 1959, 1963), who considered the configuration of the muscle origins to be of taxonomic significance and related to the progressive flattening of the anuran skull. He considered the primitive condition of the muscle to be a single slip originating from dermal bone (the otic ramus of the squamosal) as in the Bufonidae and the Atelopodidae. Starrett (1968) disagreed, considering a double origin to be the most primitive, i.e., from both fascia and cartilage or bone, because this configuration is the most common among living reptiles and amphibians. Loss of either origin would represent a more recent change. Starrett found the depressor mandibulae to be more variable within families and useful as a family character only among the bufonids, pelobatids, and ranoids. Lynch (1971) found the muscle of questionable value in leptodactylid classification. The character has been used by Limeses (1965), Heyer (1975), and Tyler and Davies (1980) at the generic and species levels.

The depressor mandibulae musculature was examined routinely in all of the specimens listed in Appendix A. There is considerable variation in configuration of this muscle complex among the hyperoliids, especially in the relative sizes of different slips. In general, however, all exhibit origins similar to those described as "DFSQAT" by Starrett (1968) and typical of ranoids, i.e., the muscle has a tripartite origin. The most posterior slip originates from the dorsal fascia, most often near the scapula (pars fascialis); the medial slip originates from the crista parotica and/or the otic ramus of the squamosal; the smallest and most anterior element arises from the posterior perimeter of the annulus tympanicus (pars tympanicus). In the majority of hyperoliids, the medial slip actually originates on the crista parotica and overlaps the squamosal. There is squamosal involvement in many species, but the results of my study indicate that this condition varies intragenerically.

The pars tympanicus is present as a distinct slip of variable size in all species examined except *Callixalus pictus,* which lacks the annulus tympanicus. In *Kassina wealei* and *K. kuvangensis,* the pars tympanicus is reduced to a few inconspicuous fibers. In one specimen of *Leptopelis hyloides,* CAS 146078, the pars tympanicus is expanded vertically and originates within the annulus tympanicus, completely obscuring the posterior margin of that structure. In others it is normal.

In most of the hyperoliids studied, the pars fascialis and the squamosal/otic component of the m. depressor mandibulae are roughly equal in size, appearing together as a single fan-shaped muscle. However, in *Chrysobatrachus cupreonitens, Opisthothylax immaculatus, Kassinula* *wittei, Kassina maculata, K. mertensi,* most members of the *K. senegalensis* complex, and *Tornierella kouniensis,* the pars fascialis is longer and broader than the squamosal/otic slip. In many species, the fibers of the two slips are surrounded by separate epimysia. In *Kassina senegalensis ovamboensis* and *Tornierella kouniensis* the two slips merge only at the point of insertion on the retroarticular process of the mandible. In the latter, there is extreme separation of the two elements, but this is undoubtedly a specialization allowing the passage of the supramandibular expansion of the m. interhyoideus (Drewes and Roth 1981).

Starrett (1968) briefly mentioned that in those frogs that lack the annulus tympanicus there is a tendency for the origin of the m. depressor mandibulae to be shifted slightly more anteriorly; such is the case with *Callixalus pictus* and in some of the Bufonidae of the *Nectophrynoides* line (A. G. C. Grandison, British Museum [Natural History], pers. comm.). Here, the anterior portion of the depressor mandibulae completely covers the area normally occupied by the annulus tympanicus. In two ranids that lack the annulus, *Arthroleptella lightfooti* and *Cacosternum boettgeri,* the muscle is normal and symmetrically fan-shaped, although the pars tympanicus is absent. In *Hemisus,* however, the muscle is oriented strongly in a posterior direction, the pars fascialis being extremely long and originating at a point posterior to the axilla of the forelimb.

In general, the depressor mandibulae musculature of the Hyperoliidae is very similar to that of the ranoids described by Starrett (1968) and those I examined. There are no clear-cut distinctions between ranids and hyperoliids in this respect.

In this study I did not examine the adductor mandibulae musculature. However, as part of a separate project (Drewes and Roth 1981), this complex and its functional significance was examined in detail in the genus *Tornierella.* The results suggest that characteristics of the adductor musculature may be of value in assessing generic relationships among the Hyperoliidae. Starrett (1968) examined but three hyperoliid taxa, *Hyperolius pusillus, H. concolor,* and *Kassina senegalensis,* and found the m. adductor mandibulae posterior subexternus absent in all adults of these species but present in the larvae (it is present in most adult ranids). Drewes and Roth (1981) have shown that the muscle is present in both *Tornierella obscura* and *T. kouniensis* and, in fact, is greatly expanded in the latter.

RESULTS AND DISCUSSION

Figure 25 is the cladogram that best represents the hypothetical phylogenetic relationships of the hyperoliid genera. It is based on the data presented above, which have been subjected to a cladistic analysis, by hand, following the principles of Hennig (1966) and character weighting as outlined by Hecht and Edwards (1977). Any hypothetical phylogeny is only accurate to the degree that the characters have been accurately examined and the sequence and polarity of their states properly interpreted. The cladogram contains one uncorroborated node (see Fig. 25). Based on the characters I examined and my interpretation of them, the Hyperoliidae is a monophyletic group including the following genera: *Leptopelis* (J), *Phlyctimantis* (M), *Kassinula* (I), *Tornierella* (N), *Kassina* (H), *Kassina wealei* (H18), *Cryptothylax* (E), *Tachycnemis* (K), *Heterixalus* (F), *Afrixalus* (B), *Hyperolius* (G), *Opisthothylax* (L), *Chrysobatrachus* (D), *Acanthixalus* (A) and *Callixalus* (C).

Intergeneric Relationships

Leptopelis. This genus is the most primitive within the family Hyperoliidae, sharing only three apomorphic character states with the rest of the hyperoliid lineages (its sister group): the unfused condition of the carpals and tarsals, and intercalary elements (see Liem 1970 for characters not examined here). *Leptopelis* apparently diverged from the ancestral hyperoliid stock very early, a conclusion also reached by Laurent (1951) and Liem (1970).

The kassinoid genera: An early divergent lineage is represented by the kassinoid genera, which are distinguished from the rest of the hyperoliids by four derived character states. *Phlyctimantis* appears to be the most primitive kassinoid genus, as it possesses no derived character states to differentiate it. Laurent (1976) suggested that the genus *Kassina* "originates probably from the completely terrestrial adaptation of any population of *Phlyctimantis.*" *Phlyctimantis* shares a sister-group relationship (common ancestry) with the other kassinoids, which tends to support Laurent's hypothesis.

The results of this study indicate that as cur-

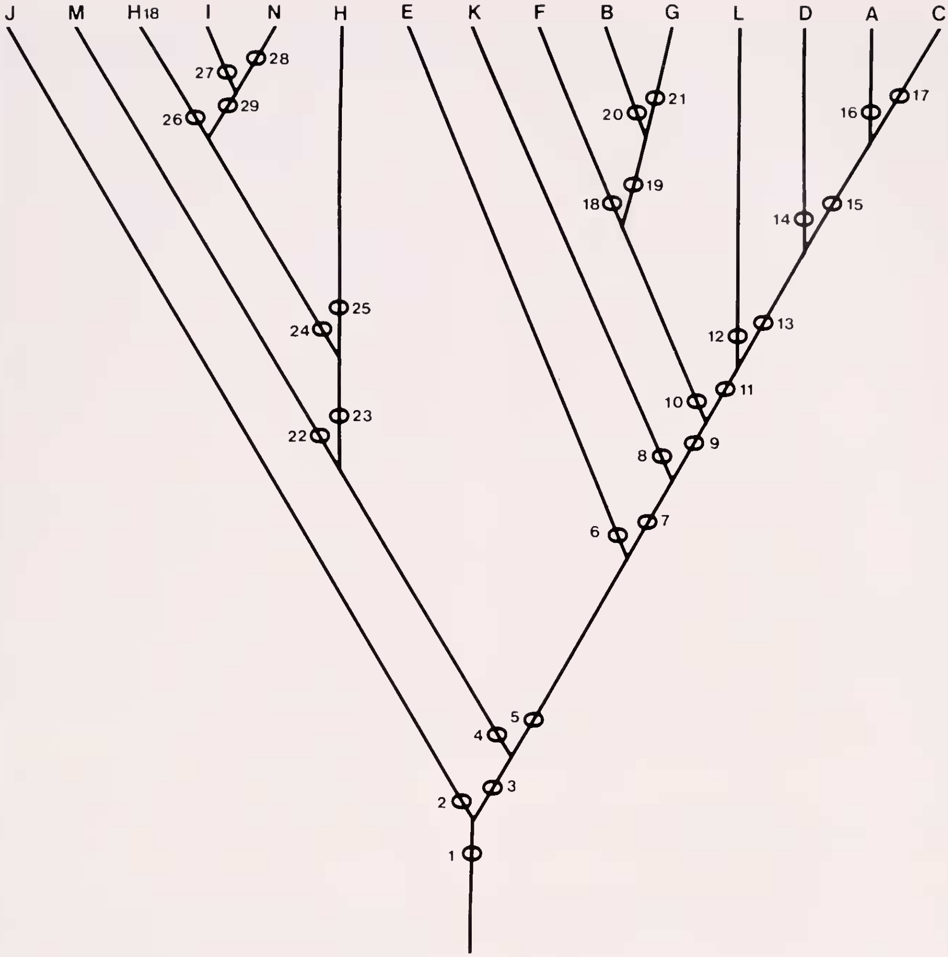

FIGURE 25. Dendrogram showing hypothetical relationships of genera of Hyperoliidae as proposed by this study. Abbreviations are as in text and Appendix B. Nodes are indicated by horizontal ovals; each is numbered. Each node represents an evolutionary change to one or more derived character states. Character states are listed for each node below, such as 30^2, i.e., character state 2 of character number 30 (see text).

Key: **1)** 26^2, 27^2; **2)** 1^2, 14^1; **3)** 10^1, 11^1, 16^3, 18^3, 19^1, 20^1, 24^3; **4)** 1^1, 7^1, 18^6, 21^6; **5)** 2^1; **6)** 9^1, 17^2, 18^4, 21^1; **7)** 3^2, 4^1, 6^1; **8)** 1^2, 9^1, 24^1; **9)** 1^0, 20^2; **10)** 18^5; **11)** 23^4, 24^2; **12)** 3^0, 14^1; **13)** 18^2; **14)** 12^2, 22^0; **15)** 5^1. 20^3, 21^0; **16)** 9^1, 14^4, 18^1; **17)** 7^1, 16^2, 24^2; **18)** 9^0, 14^1; **19)** 21^2; **20)** 7^1; **21)** 22^0, 23^0; **22)** uncorroborated node; **23)** 20^2; **24)** 12^2; **25)** 12^0; **26)** 4^1, 8^1, 9^0; **27)** 2^1, 3^2, 6^1, 8^1, 9^0, 13^0, 14^1, 23^2, 24^1; **28)** 3^1, 4^1, 7^2, 11^0, 16^2, 21^7; **29)** 1^0, 15^1, 23^0.

rently recognized, the genus *Kassina* is paraphyletic if *K. wealei* is included. There are four synapomorphies that place *K. wealei* in the lineage including *Kassinula* and *Tornierella*, and this lineage is the sister group of the remaining species of *Kassina*. *Kassinula* and *Tornierella* are here considered to represent valid genera. The status of *Kassina wealei* will be examined in a subsequent study. *Tornierella* and *Kassinula* appear to be the most derived of the kassinoid line and are interpreted here as sister groups. The kassinoids are treated in more detail in the next section.

Cryptothylax. This taxon is distinct from the remaining hyperoliid lineages on the basis of four apomorphic character states. Liem (1970) considered *Cryptothylax* to be closely related to *Phlyctimantis*. *C. minutus* Laurent was not examined.

Tachycnemis. The monotypic Seychelles endemic, *Tachycnemis,* exhibits three apomorphic character states that differentiate it from its sister group, the remaining hyperoliids (Fig. 25). Although *Tachycnemis* is superficially similar to *Leptopelis,* the two are apparently not closely related. A subsequent examination including comparisons of breeding biology may alter this conclusion.

Hyperolius, Heterixalus, and Afrixalus. These genera, which together comprise the bulk of hyperoliid species (approximately 155), constitute a monophyletic lineage distinguished from the remaining members of the family by three derived character states. Based on the characters examined here, *Heterixalus* represents the sister group of *Hyperolius* and *Afrixalus* and is differentiated from them by the possession of two apomorphic character states. *Heterixalus* is extremely similar to *Hyperolius* (see generic diagnosis). Its members have been studied by Rose Blommers-Schlösser (1982) of The Netherlands. *Afrixalus* is interpreted here as the sister group of *Hyperolius.* They are distinguished from each other by their derived character states, one in *Afrixalus,* two in *Hyperolius* (Fig. 25). Liem (1970) also found close relationship between these two taxa.

Opisthothylax, Chrysobatrachus, Acanthixalus, and Callixalus. The remaining four genera are monotypic, highly derived, and rather limited in distribution. *Opisthothylax* is distinguished by two apomorphic characteristics as is *Chrysobatrachus. Acanthixalus* and *Callixalus* appear to be sister groups. *Acanthixalus* demonstrates three derived character states, and *Callixalus,* four.

Intrageneric Relationships

One of the initial goals of this study was to contribute to the knowledge of the evolutionary relationships of the species within the genera *Leptopelis, Afrixalus, Hyperolius* and the kassinoids. It became apparent that the characters chosen were inappropriate for analysis at the species level in *Leptopelis* and *Afrixalus,* and that the number of species sampled was inadequate to draw meaningful conclusions in *Hyperolius.* A number of potentially significant trends have been noted, however, and these will be investigated in subsequent work. In the kassinoid group, though, all presently recognized species, except *Phlyctimantis keithae* Schiøtz, were available and were examined, including almost all subspecies of the confusing *Kassina senegalensis* complex (see Schiøtz 1975; Laurent 1976). The kassinoid species were analyzed cladistically. Figure 26 represents a cladogram of the hypothetical phylogenetic relationships within this group. The cladogram contains two uncorroborated nodes. The kassinoid lineages are characterized by the possession of five synapomorphies.

Phlyctimantis. The generic position of this taxon with respect to other kassinoids has been suggested above. The only distinction between *Phlyctimantis leonardi* and *P. verrucosus* revealed by this study is that members of *P. verrucosus* possess the more derived condition of the metasternum.

Kassinula. *Kassinula wittei* is a species hitherto included in the genus *Kassina* (see Schiøtz 1975). It is a minute, apparently paedomorphic form which shares a sister group relationship with *Tornierella. K. wittei* possesses nine apomorphic character states that distinguish it from *Tornierella.* These characteristics, together with several not included in the cladistic analysis, suggest that *K. wittei* deserves generic status; they are described in the generic analysis.

Tornierella. This taxon includes two species, *T. kouniensis* and *T. obscura,* both of which were included in the genus *Kassina* until recently (Largen 1975). Drewes and Roth (1981) have shown that on the basis of a number of skeletal and myological characters these species are morphologically (and perhaps behaviorally) specialized for feeding almost exclusively on whole snails. We resurrected the genus *Tornierella* Ahl to include them. None of the characters applied in the present study serve to separate the two species of this genus, but numerous differences exist (Largen 1975; Drewes and Roth 1981). The genus *Tornierella* is distinguished from its sister group *Kassinula* by six apomorphic character states (Fig. 26).

***Kassina wealei* (H18).** *K. wealei* is currently included in the genus *Kassina,* yet the results of this study indicate four derived character states that require, within the framework of the characters utilized here, its recognition as the sister group of *Kassinula* and *Tornierella.* Inclusion of this species in *Kassina* renders the latter taxon paraphyletic. I do not consider the character states separating *K. wealei* to be of high weight, yet many of those that characterize the *Tornierella/*

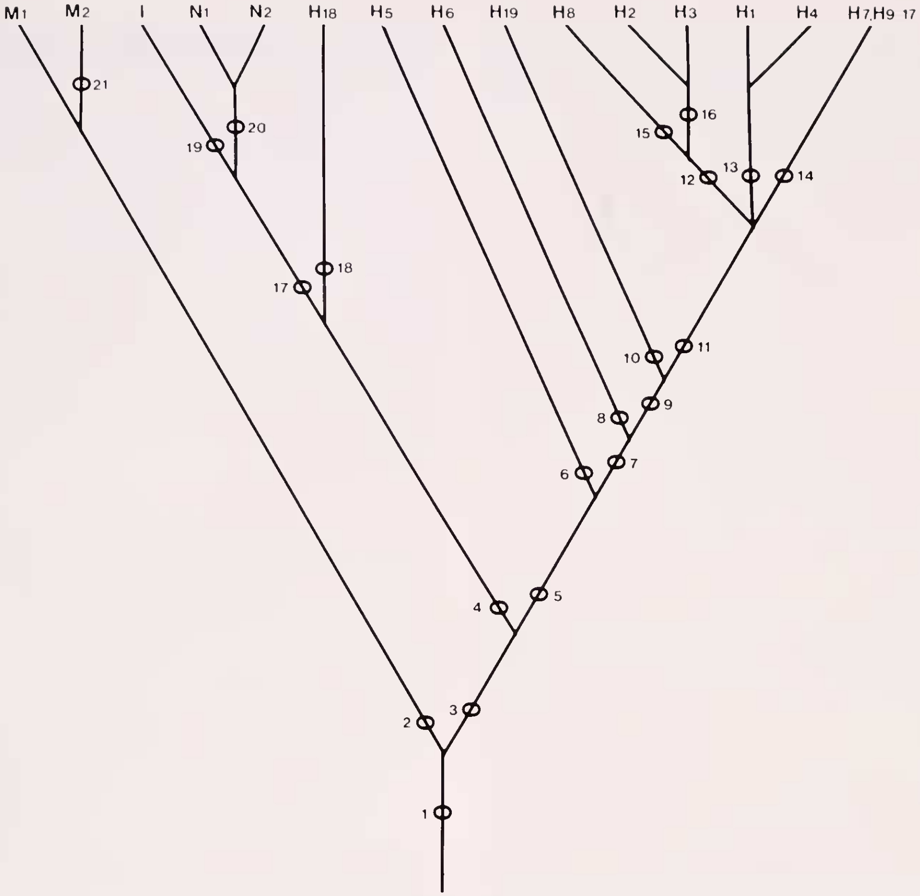

FIGURE 26. Dendrogram showing hypothetical phylogenetic relationships of kassinoid genera of the family Hyperoliidae proposed in this study. Abbreviations and character states as in text; nodes as in Fig. 16. Node 1 in this cladogram corresponds to node 4 in Fig. 16.

Key: **1)** 1^1, 7^1, 13^1, 18^6, 21^6; **2)** uncorroborated node; **3)** 20^2; **4)** 12^2; **5)** 12^0; **6)** 17^0; **7)** 1^1, 18^7; **8)** 3^2, 8^1, 14^2, 17^0, 20^1; **9)** uncorroborated node; **10)** 1^0, 7^0, 12^1, 17^2; **11)** 14^4; **12)** 4^1; **13)** 11^4, 12^0; **14)** 2^1; **15)** 1^1; 3^2; **16)** 7^2, 12^1, 17^0; **17)** 1^0, 15^1, 23^1; **18)** 4^1, 8^1, 9^0; **19)** 2^1, 3^2; 6^1, 8^1, 9^0, 13^0, 14^1, 23^2, 24^1; **20)** 17^2.

Kassinula lineage and the rest of the kassinoids are important, and they are not shared by *K. wealei.* Additional characteristics not analyzed here separate *K. wealei.* The larval tooth formula differs from that of most other members of the genus, and Tandy and Drewes (*in press*) have shown that the structure of the mating call is different from that of most other species in the genus, being more similar to the call of *Kassinula wittei* (I) and *K. kuvangensis* (H5), the least derived member of the genus *Kassina* (see below). Having adopted the principles and conditions of phylogenetic systematics (Hennig 1966) for the analysis of this group, I am bound to accept that *K. wealei* is a separate taxon of generic rank, especially as I feel secure in the status of other genera in its lineage (*Tornierella* and *Kassinula*). However, the characters I have examined do not permit me to describe it as a separate genus. The status of *K. wealei* will be investigated in more detail and with additional characters in a subsequent study. For purposes of communication, it is held in abeyance in the genus *Kassina.*

Kassina. This is the most polymorphic genus in the family Hyperoliidae. The least-derived species appears to be *K. kuvangensis,* having only

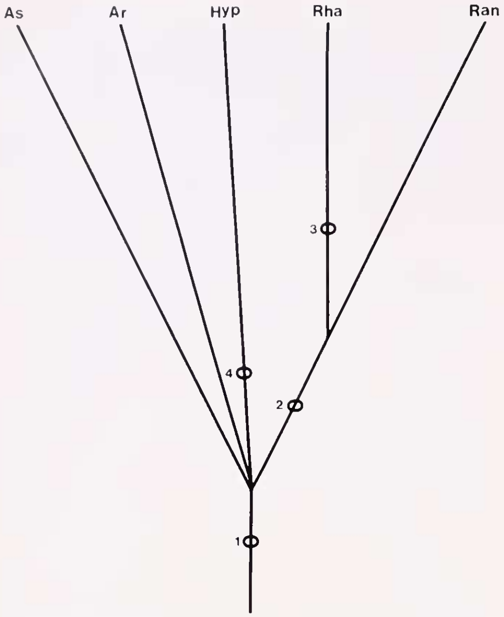

FIGURE 27. Representation of proposed familial relationships of Hyperoliidae to other African ranoids. Abbreviations are as in text; RAN represents Ranidae examined in this study only.

Key: **1)** 25^0, 26^1, 27^1; **2)** 25^1, 28^1; **3)** 24 (states unknown); **4)** 26^2, 27^2.

a single apomorphic character state differentiating it from the rest of the genus. Tandy and Drewes (*in press*) have shown that the mating call of members of this species is similar to the calls of *Kassinula wittei* and *K. wealei*. *K. lamottei* (H6) is separated from its sister group, the remaining *Kassina*, by the possession of five derived character states.

Following Laurent and Combaz (1950), *Kassina maculata* (H19) was the sole survivor in the genus *Hylambates*, which along with *Megalixalus* was one of the "catch-all" taxa of Old World treefrogs. *Hylambates* has been suppressed in favor of *Kassina* (Laurent and Smith 1966). The results of my study suggest that this taxon is indeed a member of the genus *Kassina*—Liem's results (1970) and Laurent's ideas about limb proportions (1976) notwithstanding. *Kassina maculata* has four apomorphic character states which delineate it from the remaining species (the sister group).

Analysis of the remaining members of the genus *Kassina* has resulted in an unresolved trichotomy (see Fig. 26): (1) *K. parkeri* (H8) appears to share a sister group relationship with the two arboreal sister species *K. cochranae* (H2) and *K. decorata* (H3); *K. parkeri* is distinct from *K. cochranae* and *K. decorata* on the basis of two derived character states, they are distinct from *K. parkeri* on the basis of three. The members of this lineage share one derived character state. (2) *Kassina cassinoides* (H1) and *K. fusca* (H4) are sister species based on one unique synapomorphy. (3) *Kassina mertensi* (H7) and *K. senegalensis* (including all of its subspecies H9–H17) are inseparable cladistically; they cannot be related cladistically to either of the other two lineages on the basis of the characters I have analyzed.

Family Relationships

Figure 27 represents the cladistic relationships of the family Hyperoliidae to the other ranoids examined, based on the characters studied. I consider the hyperoliids a monophyletic, highly evolved group on the assumption that the characters distinguishing it from all other ranoids—the presence of unfused carpalia (char. 26^2) and tarsalia (char. 27^2)—are apomorphic states, and that these states are the result of paedomorphic reversal. I have been unable to confirm the presence of these character states in any other ranoids examined. I find it highly unlikely that so derived a group of treefrogs would retain characters shared otherwise by distantly related primitive groups, and even by fossil forms (Jarŏsová 1973, 1974). As demonstrated in the preceding sections, the hyperoliids exhibit a number of characteristics that may be interpreted as paedomorphic, side by side with highly derived character states including autapomorphies.

Paedomorphic processes are being examined (Alberch et al. 1979), but paedomorphic characteristics have yet to be successfully interpreted in systematic studies (Hecht and Edwards 1977). I have adopted the philosophy of Hennig (1966) that any evolutionary change (including reversals) must be considered derived. Ontogenetic evidence is unavailable for the characters I have examined.

A cartilaginous metasternum is shared by arthroleptines, astylosternines, and the Hyperoliidae. However, I interpret this state to be primitive and therefore cannot use it to infer monophyly for these groups. At present it seems best to represent familial relationships as in Figure 27, wherein there is a basal unresolved tetrachotomy.

The family Ranidae (RAN) is poorly understood and may be paraphyletic or even polyphyletic. However, it appears to share common ancestry with the Rhacophoridae (RHA), as evidenced by synapomorphy of two character states.

Laurent (1978, 1979) insisted on a close relationship between the hyperoliids (HYP), the Arthroleptinae (AR), and Astylosterninae (AS), based on what he termed "resolutely cladistic" interpretations (1978). In fact, he actually considered the above characters to be primitive (1979). Relationship cannot be demonstrated by symplesiomorphy (Hennig 1966), thus his view is unsupported.

In this study, I have examined *Hemisus* and several species of arthroleptine and astylosternine ranids for comparison to the Hyperoliidae, but I have not attempted to assess relationships between them. I am unable, therefore, to address Laurent's placement of *Hemisus* in a distinct family, the Hemisidae (1979). I can conclude, however, that *Hemisus* does not belong with the Ranidae (see Fig. 27, node 2), nor with the Hyperoliidae.

The astylosternine lineage is distinct from the rest of the African ranoids in possessing direct development (in *Arthroleptis*) and, at least in this regard, should be considered specialized but with relationships close to the ancestral ranoid stock. A diagnosis of this group is beyond the scope of this study.

Since the completion of my analyses, Dubois (1981) placed both the astylosternine and arthroleptine ranids as subfamilies within the family Arthroleptidae and followed Laurent (1979) in recognizing the Hemisidae.

Finally, I must emphasize that my estimate of the relationships of the Hyperoliidae is based solely on comparison with the other ranoids included in this study and with data in the literature. I have not examined platymantine or scaphiophrynine ranoids.

Systematic Accounts

The following section includes a diagnosis of the family Hyperoliidae, a key to the genera, and descriptions and diagnoses of each genus recognized in this study.

Each diagnosis is followed by a section on the natural history of members of the genus, including breeding biology, vocalization, karyology, and larval morphology. This is followed by a list of the species currently recognized in each genus and a description of the distribution of the genera.

Family **HYPEROLIIDAE** Laurent

Hylae: Tschudi, 1838:25, 27 (part.).

Hylina: Hoffmann, 1873–1878:646 (part.).

Hylaeformes: Duméril and Bibron, 1841:491 (part.); A. Duméril, 1853:137 (part.); Duméril et al., 1854:400 (part.).

Hylodidae: Hoffmann, 1873–1878:650 (part.).

Cystignathidae: Günther, 1858:26 (part.).

Raniformes: Duméril and Bibron, 1841:317 (part.).; Duméril et al., 1854:392 (part.); Cope, 1864:181 (part.).

Ranidae: Cope, 1864:182 (part.); 1865:114 (part.); 1867:198 (part.); Boulenger, 1882:3 (part.); 1888:204 (part.); Gadow, 1901:237 (part.); Roux, 1905:777 (part.); Nicholls, 1916:87 (part.); Noble, 1922:22 (part.); Ahl, 1923:1 (part.); Noble, 1924:183 (part.).

Raninae: Peters, 1882:142 (part.); Gadow, 1901:238 (part.).

Polypedetidae: Günther, 1858:70 (part.); Mivart, 1869:292 (part.); Hoffman, 1873–1878:646 (part.); Boettger, 1881b:540 (part.); Peters, 1882:21 (part.); Ahl, 1931:1 (part.); Noble 1931:515 (part.); Laevit, 1932:178 (part.); Monard, 1937:31.

Discophidae: Ahl, 1924:269 (part.).

Rhacophoridae: Hoffman, 1932:562 (part.); Parker, 1934:9 (part.); deWitte, 1941:94; Laurent, 1941a:86 (part.); 1944:110 (part.); Loveridge, 1957:314 (part.); Schmidt and Inger, 1959:176 (part.); Inger, 1967:380–81 (part.); Schiøtz, 1967:11 (part.).

Hyperoliidae: Laurent, 1951b:117 (part.); Perret, 1966:376 (part.); Dowling and Duellman, 1978:44.1; Laurent, 1979a:419.

Hyperoliinae: Laurent and Combaz, 1950:269; Laurent, 1951b:119; Perret, 1966:399; Laurent, 1979a:419.

Type Genus.—*Hyperolius* Rapp.

Diagnosis and Description.—Small to large treefrogs (15–82 mm snout-vent length), skin usually smooth except in *Acanthixalus*; digital tips usually dilated; transverse groove on digital pad absent; gular gland present except in *Leptopelis*; pectoral, forearm or digital glands present in most genera; vocal pouch present except in *Leptopelis*, *Cryptothylax*, *Acanthixalus* and *Callixalus*; vocal sac present except in *Acanthixalus* and *Callixalus*; keratinized nuptial pads absent in males except in *Cryptothylax* and *Phlyctimantis*; vocal sac openings usually anterior, occasionally lateral slits involving anterior horn of hyoid except in *Leptopelis*; pupils horizontal or vertical.

Pectoral girdle firmisternal; metasternum usually a broad, occasionally a narrow, cartilaginous plate; omosternum moderately to broadly forked except in *Leptopelis*; intercalary elements present; metacarpals usually slightly dilated distally; disto-medial end of third metacarpal with bony knob; third carpal always free; second tarsal always free; sacral diapophyses cylindrical to moderately dilated; vertebral column usually diplasiocoelous, procoelous in *Callixalus* and *Acanthixalus*; vertebral column usually elongated; neural arches usually nonimbricate except in *Cryptothylax, Kassina, Phlyctimantis,* and *Tornierella*; coccyx always bicondylar; occipital condyles always widely spaced; sphenethmoid usually unfused ventrally, slightly to moderately exposed dorsally (except in *Leptopelis* and *Tachycnemis*).

Posterolateral process of hyoid absent except in *Kassina wealei, Acanthixalus, Cryptothylax, Kassinula,* and *Heterixalus*; cartilaginous stalk of thyrohyal present except in *Leptopelis*; elements of anterior horn of ceratohyal present except in *Leptopelis*; alary process always present.

External slip of m. geniohyoideus lateralis either inserting on thyrohyal or on posterior edge of alary process; usually two slips of m. petrohyoideus posterior present, three in *Kassina* and *Leptopelis*; aponeurosis palmaris usually present, except in *Chrysobatrachus, Kassina wealei, Kassinula,* and *Tornierella*; distal ends of m. palmaris longus divided in most and communicating directly with third and fourth tendenes superficialis through aponeurosis palmaris, except in some *Kassina*; m. humerodorsalis consisting of two divided slips; m. adductor longus present except in *Leptopelis*; m. tensor fasciae latae present except in *Kassinula*; m. extensor digitorum communis longus usually consisting of one slip inserting on proximal part of third metatarsal; m. cutaneous pectoris always absent; m. depressor mandibulae usually united, fan-shaped, except in *Kassina*.

Content of the Family.—*Leptopelis* Günther, *Phlyctimantis* Laurent and Combaz, *Kassina* Girard, *Kassinula* Laurent, *Tornierella* Ahl, *Kassina wealei* (see Fig. 17), *Cryptothylax* Laurent and Combaz, *Tachycnemis* Fitzinger, *Heterixalus* Laurent, *Afrixalus* Laurent, *Hyperolius* Rapp, *Opisthothylax* Perret, *Chrysobatrachus* Laurent, *Acanthixalus* Laurent, and *Callixalus* Laurent.

Distribution.—Afrotropical region (Crossky and White 1977) and the Seychelles Islands.

A Key to the Genera of the Hyperoliidae
(based on preserved adult males)

1a. Pupil horizontal or round 2
1b. Pupil vertically elliptical or rhomboidal 4

2a. Gular gland a single structure (unpaired) 3
2b. Gular glands paired longitudinal ovals situated near angle of jaws; vocal pouch absent .... *Acanthixalus*

3a. Gular gland a transverse oval with indistinct or broken anterior margin, situated in posterior portion of gular region; vocal pouch absent .... *Chrysobatrachus*
3b. Gular gland round, oval or rhomboid, more or less central with lateral and posterior margins usually free; vocal pouch present, composed of extensive folds of skin .... *Hyperolius*

4a. Gular gland present 5
4b. Gular gland absent (pectoral glands often present) .... *Leptopelis*

5a. Gular gland overlies densely pigmented (blackish) pockets of vocal pouch (visible under lateral margins of gland 11
5b. Blackish tissue absent from gular gland/vocal pouch apparatus 6

6a. Gular gland very large, obscuring the entire gular region, often overlapping lateral margins of lower jaws; vocal pouch absent .... *Cryptothylax*
6b. Gular gland smaller than above 7

7a. Vocal pouch absent; gular gland a transverse oval, situated in posterior portion of gular region .... *Callixalus*
7b. Vocal pouch present 8

8a. Vocal pouch simple, composed of unfolded skin; gular gland a medio-posterior disc with edges not free 9
8b. Vocal pouch composed of extensive folds of skin, overlain by gular gland; gland round, oval or rhomboidal with lateral and posterior edges usually free 10

9a. Tympanum present; adults large (to 70 mm); endemic to Seychelles Archipelago .... *Tachycnemis*

9b. Tympanum absent; adults smaller (to 33 mm); West African .... *Opisthothylax*

10a. Tympanum usually distinct; toes usually half-webbed; skin of head, dorsum and hind limbs usually beset with minute, dark-tipped spinules; African ..... *Afrixalus*
10b. Tympanum usually indistinct or absent; toes usually fully webbed; skin of head, dorsum, and hind limbs smooth; endemic to Madagascar .... *Heterixalus*

11a. Gular gland a thick, round disc with posterior and lateral edges free 12
11b. Gular gland thick, strap-shaped, with anterior and posterior margins fixed, lateral edges free 13

12a. Hind limbs long, gracile; tympanum present .... *Phlyctimantis*
12b. Hind limbs short, stout; tympanum indistinct or barely visible; a yellowish inguinal patch present (sharply defined in *T. obscura*) .... *Tornierella*

13a. Tympanum absent; minute (adults to 22 mm); dorsal pattern consisting of unbroken, convergent stripes .... *Kassinula*
13b. Tympanum present; larger (over 35 mm); dorsal pattern usually not stripes (except *K. cassinoides*) or if so, stripes discontinuous .... *Kassina*

Acanthixalus Laurent

Hyperolius: Buchholz and Peters *in* Peters, 1875:208 (part.); Boulenger, 1882:130 (part.); Ahl, 1931:422 (part.).

Megalixalus: Boulenger, 1882:128 (part.); Nieden, 1910:57 (part.); Noble, 1924:270 (part.); Ahl, 1930c:89 (part.); 1931:422 (part.).

Acanthixalus: Laurent, 1944:111; Laurent and Combaz, 1950:277; Perret, 1962:90; 1966:446; Schiøtz: 1967:134; Liem, 1970:112.

Nesionixalus: Perret, 1976:34.

Type Species.—*Megalixalus spinosus* (Buchholz and Peters); by designation of Laurent, 1944.

Diagnosis.—Medium-sized frogs (snout-vent length 32–36 mm); pupil horizontal; gular glands paired longitudinal ovals; tarsal spines present; tympanum absent; vertebrae procoelous; posterolateral process of hyoid present.

Description.—Body stout but flattened; dorsal skin and limbs strongly warty, with tarsal spines present; finger and toe tips greatly dilated, dilations broader than long; fingers one-third webbed; toes one-half webbed; gular glands paired longitudinal ovals situated near angle of jaws; forearm, digital and pectoral glands absent; vocal pouch absent; vocal sac openings absent. Pupil horizontal; nuptial pads absent; tympanum absent.

Nasals subtriangular, convergent, but well separated anteriorly, widely separated posteriorly and from frontoparietals; frontoparietals rectangular; quadratojugal overlapped by maxilla anteriorly; sphenethmoid unfused ventrally, not exposed dorsally; prevomerine dentigerous processes absent.

Vertebral column procoelous, not elongated; neural arches not imbricate; transverse processes of vertebrae long, those of the eighth vertebra perpendicular to vertebral axis; sacral diapophyses moderately dilated.

Medial margins of coracoids entire; omosternum broadly forked at base; metasternum cartilaginous, from 1.5 to 3.0 times broader caudally than anteriorly, caudal margins smooth, medial portion of plate may be mineralized; terminal phalanges strongly bifurcate, each branch longer than width of stem; digital subarticular sesamoids absent; intercalary elements mineralized.

Anterior horn made up of anterior (medial) and lateral branches, the latter less than one-third the length of the former; alary process present, broad-based with short stalk, distal dilation much broader than base; posterolateral process present, less than one-third as long as thyrohyal; cartilaginous stalk of thyrohyal present.

Third and fourth tendo superficiales able to slide through aponeurosis palmaris; vocal sac absent; m. depressor mandibulae fan-shaped as in *Hyperolius.*

Karyotype.—Undescribed.

Breeding Biology.—Males lack vocal sac and vocal sac openings and are apparently mute. Eggs are laid in pockets of water in holes in trees, stumps, and branch axils (Perret 1961). Number of eggs and amplexus are undescribed. Lamotte et al. (1959a) have described the tadpole as stout and darkly pigmented. A unique feature of the tadpole is in the orientation of its tail: the tail is deflected upward so that the angle formed between it and the body is 150 to 160 degrees. The larval tooth formula is 1,3+3/3 (Lamotte et al. 1959a).

Remarks.—Perret (1961) noted that *Acanthixalus* are strictly arboreal, the entire life cycle occurring in trees. Apparently, *Acanthixalus* remain in pockets of water during the day and forage at night. When disturbed, *Acanthixalus* exhibit a most remarkable response: the body is flattened, the eyes are half closed, the mouth is slightly opened, and the tongue is fully extruded. The tongue, which is left in this position for several seconds at a time, is bright orange (see photograph in Perret 1961). *Acanthixalus* have some unique characteristics such as tarsal spines, paired gular glands, and the curious shape of the greatly expanded digits. While clearly very specialized, members of this genus retain characters that are considered primitive, such as the extra supralabial tooth rows in the larva. *Acanthixalus* exhibit the procoelous condition of the vertebrae.

CONTENT OF THE GENUS.—*Acanthixalus spinosus* (Buchholz and Peters).

DISTRIBUTION.—Forests of southern Nigeria and Cameroun to northeastern Zaire.

Afrixalus Laurent

Euchnemis (*sic*): BIANCONI, 1850:23.

Hyperolius: PETERS, 1855:56 (part.); GÜNTHER, 1858:85; NOBLE, 1924:250 (part.).

Rappia: GÜNTHER, 1868:479 (part.); BOULENGER, 1882:119 (part.).

Megalixalus: GÜNTHER, 1868:485; BOULENGER, 1882:128; 1888: 205 (part.); NIEDEN, 1910:57 (part.); NOBLE, 1924:270 (part.); AHL, 1930c:89 (part.); 1931:422 (part.); LAURENT, 1944:110 (part.).

Afrixalus: LAURENT, 1944:113; 1950a:14; LAURENT AND COMBAZ, 1950:277; LAURENT, 1951c:23; PERRET, 1966:439; SCHIOTZ, 1967:98; 1975:72; LIEM, 1970:108.

TYPE SPECIES.—*Megalixalus fornasinii* BIANCONI, by original designation.

DIAGNOSIS.—Small frogs (snout-vent length 20–35 mm); pupil vertical; skin of males usually spinulous; tympanum usually distinct; toes usually half-webbed; posterolateral process of hyoid absent.

DESCRIPTION.—Body elongated; skin of body and limbs of males usually covered with minute spinules; distal segment of digit and its digital pad similar to *Hyperolius*; fingers up to two-thirds webbed; toes half-webbed. Gular gland a disc, oval or rhomboid; forearm, digital, and pectoral glands absent; vocal pouch similar to *Hyperolius*; vocal sac openings similar to *Hyperolius*; nuptial pad absent; pupil vertical; tympanum present or intraspecifically variable.

Nasals triangular, in contact medially; quadratojugal variable—in contact with maxilla (*A. congicus*), overlapped by maxilla or reduced or absent (*A. brachycnemis, A. weidholzi*); dorsal exposure of sphenethmoid not extensive; sphenethmoid unfused ventrally; frontoparietals rectangular, narrowly separated; palatines not dilated at medial end, not reaching maxilla; prevomerine dentigerous processes absent; terminal phalanges peniform; digital subarticular sesamoids absent; intercalary elements peripherally mineralized in adults.

Anterior horn consisting of medial and lateral branches, the latter at least one-third as long as the former; alary process present with broad base, distal dilation equal to or slightly broader than base; posterolateral process absent.

Medial margins of coracoids entire; vertebral column moderately elongated; neural arches not imbricate; transverse processes of eighth vertebra usually angled markedly forward; sacral diapophyses slightly dilated; omosternum broadly forked at base; metasternum 0.5–1.5 times broader posteriorly than anteriorly, stem and medial portions of plate sometimes mineralized.

M. geniohyoideus lateralis inserting on thyrohyal; some fibres sometimes inserting on hyoid plate; m. petrohyoideus posterior consisting of two slips; vocal sac composed of anterior and posterior development of m. interhyoideus, the former comprising no more than one-third of the superficial mandibular musculature, the latter not extending posteriorly as far as pectoral musculature; palmaris complex similar to that of *Hyperolius*; m. adductor longus present; m. extensor digitorum communis longus short, inserting on proximal portion of metatarsal of third toe; m. depressor mandibulae similar to that in *Hyperolius*.

KARYOTYPE.—Now known for 5 species, 2n = 24, apparently most similar in morphology to *Kassina* in size disparity between pairs one and two (Scheel 1973; Bogart and Tandy 1981).

BREEDING BIOLOGY.—Males call from low bushes, reeds, and sedges (Schiøtz 1967, 1974). Many calls have been sonographed and analyzed; the typical *Afrixalus* voice is described as a "repercussion of identical figures." In many West African species the call consists of two motifs: first a low creaking, followed by a series of rapid clicks (Schiøtz 1975). Calls have also been described as a "prolonged buzzing" (Schiøtz 1974) and as the "stuttering of a minute machinegun" (Wager 1965). Sonographs are presented in Schiøtz (1967, 1975) and Passmore and Carruthers (1979).

From 10 to 80 small unpigmented eggs are deposited in a thick jelly, within the fold of a leaf, which is held together by the jelly. The nest is formed either above or below the surface of still water (Wager 1960; Schiøtz 1963, 1967, 1975). Except for the absence of foam, the nests of *Afrixalus* are quite similar to *Opisthothylax* (Amiet 1974a).

Tadpoles are typified by a long, low tail and "sharklike" appearance, and reduction of mouthparts. In the known species, the larval tooth formula is 0/0 or 0/1 (Guibé and Lamotte 1958; Schiøtz 1963, 1967, 1975; Wager 1960, 1965).

REMARKS.—*Afrixalus* are arboreal and usually nocturnal. *Afrixalus brachycnemis* are apparently often found during daylight hours in exposed positions (Passmore and Carruthers 1979). Members of this genus exhibit a strong tendency toward reduction in elements of the skull such as the quadratojugal (absent in *A. brachycnemis* and *A. weidholzi* [Laurent 1944]). A frontoparietal fontanelle is present in some forms, but it is always much less pronounced than in *Kassinula*. See Amiet (1974a) for a comparison between *Opisthothylax* and *Afrixalus* breeding biology.

CONTENT OF THE GENUS.—The genus contains at least 24 species which include *A. brachycnemis* (Boulenger), *A. clarkei* Largen, *A. dorsalis* (Peters), *A. enseticola* Largen, *A. equatorialis* (Laurent), *A. fornasini* (Bianconi), *A. fulvovittatus* (Cope), *A. lacteus* Perret, *A. laevis* (Ahl), *A. leucostictus* Laurent, *A. lindholmi* (Andersson), *A. nigeriensis* Schiøtz, *A. orophilus* (Laurent), *A. osorioi* (Ferraira), *A. paradorsalis* Perret, *A. pygmaeus* (Ahl), *A. schneideri* (Boettger), *A. spinifrons* (Cope), *A. stuhlmanni* (Pfeffer), *A. sylvaticus* Schiøtz, *A. uluguruensis* Barbour & Loveridge, *A. vittiger* (Peters), *A. wiedholzi* (Mertens) and *A. wittei* (Laurent).

DISTRIBUTION.—Tropical Africa, south to Cape Province, South Africa.

Callixalus Laurent

Callixalus: LAURENT, 1950a:5; LIEM, 1970:113.

TYPE SPECIES.—*Callixalus pictus* LAURENT; by original designation.

DIAGNOSIS.—Medium-sized frogs (snout-vent length 27–36 mm); pupil vertical; gular gland a horizontal oval; vocal sac absent; tympanum absent; annulus tympanicus and columella greatly reduced; vertebral column procoelous.

DESCRIPTION.—Body slender; dorsal skin warty; digital tips dilated; webbing of fingers reduced; toes half webbed; gular gland a horizontal oval, reduced anteromedially, restricted to posterior part of gular region; forearm glands present, digital and pectoral glands absent; vocal pouch absent; vocal sac openings absent. Pupil vertical, nuptial pads absent, tympanum absent.

Nasals triangular, reduced, well separated medially and from the frontoparietals; frontoparietals rectangular; quadratojugal overlapped by maxilla anteriorly; sphenethmoid not exposed dorsally; sphenethmoid unfused ventrally; prevomerine dentigerous processes absent; annulus tympanicus reduced to incomplete ring; columella reduced, not extending beyond ventral ramus of squamosal laterally.

Medial margins of coracoids entire; vertebral column procoelous and moderately elongated; neural arches not imbricate; articular surfaces of vertebral centra notched ventrally; sacral diapophyses slightly dilated; transverse processes of eighth vertebra perpendicular to vertebral axis; omosternum moderately forked at base; metasternum cartilaginous, 1.5 times broader caudally than anteriorly, stem partially mineralized; terminal phalanges peniform; digital subarticular sesamoids absent; intercalary elements peripherally mineralized.

Medial and lateral branches of anterior horn present, the latter at least one-third as long as former; posterolateral process absent; cartilaginous stalk of thyrohyal present; alary process broad-based, stalk relatively long, distal dilation equal to or slightly less than width of base.

Vocal sac absent; palmaris musculature as in *Hyperolius,* the third and fourth tendo superficiales are able to slide through the aponeurosis palmaris; m. adductor longus present; m. depressor mandibulae fan-shaped, angled sharply forward so that anterior portion covers area normally occupied by annulus tympanicus, pars tympanicus absent.

KARYOTYPE.—Undescribed.

BREEDING BIOLOGY.—*Callixalus* lack vocal sacs and vocal sac openings. The tympanum is absent, the annulus tympanicus is vestigial, and the columella is reduced; thus it seems reasonable to assume that males of this genus have no breeding call. Nothing is known of amplexus, eggs, deposition sites, or larvae.

REMARKS.—*Callixalus* inhabit the broken stalks of bamboo from 2 to 4 m above ground in bamboo forests (Laurent 1964). Reduction of the plectral apparatus, along with other morphological features listed above, suggest that *Callixalus* is a highly derived treefrog. It is one of only two taxa among the Hyperoliidae exhibiting the procoelous condition of the vertebral centra.

Content of the Genus.—*Callixalus pictus* Laurent.

Distribution.—Found only in the Itombwe Highlands of eastern Zaire and in mountains of western Rwanda.

Chrysobatrachus Laurent

Cardioglossa: Nieden, 1908:661.
Chrysobatrachus: Laurent, 1951a:376; Liem, 1970:113.
Type Species.—*Chrysobatrachus cupreonitens* Laurent; by original designation.

Diagnosis.—Small frogs with marked sexual dimorphism (snout-vent length 20–30 mm; males about 69% female length); pupil horizontal; short hindlimbs; gular gland in males a horizontal oval; vocal pouch absent; tympanum absent; lumbar amplexus.

Description.—Dorsal skin shagreened; body robust; hind limbs very short; fingers one-third webbed; toes one-half webbed; digital tips moderately dilated; gular gland usually a horizontal oval, often reduced anteromedially, confined to posterior portion of gular region; forearm and pectoral glands present; digital glands absent; vocal pouch absent; vocal sac openings paired anterior slits, their medial margins formed by distal margins of lateral processes of anterior horn. Pupil horizontal, nuptial pads absent, tympanum absent.

Nasals triangular, well separated medially and from frontoparietals posteriorly; frontoparietals slightly narrower anteriorly than posteriorly; quadratojugal overlapped by maxilla anteriorly; sphenethmoid slightly visible anteriorly, unfused ventrally; prevomerine dentigerous processes present, prevomerine teeth absent.

Medial margins of coracoids entire; vertebral column diplasiocoelous, not elongate; sacral diapophyses slightly dilated; neural arches not imbricate; transverse processes of eighth vertebra perpendicular to vertebral axis; omosternum sexually dimorphic—moderately forked at base in males, greatly forked in females, in both sexes right arm shorter than left skewing omosternum slightly to right; metasternum cartilaginous, 1.5 times broader caudally than anteriorly, not mineralized; terminal phalanges unmodified; digital subarticular sesamoids absent; intercalary elements mineralized.

Anterior (medial) and lateral branches of anterior horn present, the latter at least one-third as long as former; posterolateral process absent; cartilaginous stalk of thyrohyal present; alary process with broad base and long stalk, distal dilation equal to or slightly greater than width of base.

Vocal sac composed of posterior development of m. interhyoideus, slightly bilobular, lobes not extending beyond anterior margins of m. supracoracoideus; aponeurosis palmaris absent, m. palmaris profundus inserting directly on proximal portion of third and fourth tendo superficiales; pars facialis of m. depressor mandibulae longer and broader than squamosal/otic component, the two well separated.

Karyotype.—Undescribed.

Breeding Biology.—*Chrysobatrachus* are unique among the Hyperoliidae in exhibiting lumbar amplexus, a phenomenon that Laurent (1964) attributed to evolutionary reversal, suggesting that it is due to the small size of the males and their inability to "grasp females at chest level," rather than to the retention of a primitive characteristic (see also Nussbaum 1980b). Nothing is known of the call, eggs, deposition sites, larvae, or larval development.

Remarks.—Apparently *Chrysobatrachus* are strictly terrestrial grassland inhabitants, commonly found some distance from water. Laurent (1964) suggested a close relationship to *Hyperolius,* based on skeletal features, and cited the absence of other terrestrial anura in the area as "incentive for a treefrog to develop terrestrial habits." Similarities in gular gland structure, and other features imply some relationship with *Callixalus,* with which *Chrysobatrachus* is sympatric.

Content of the Genus.—*Chrysobatrachus cupreonitens* Laurent.

Distribution.—Endemic to grassland above 2400 m in the Itombwe Highlands of eastern Zaire.

Cryptothylax Laurent and Combaz

Hylambates: Schilthuis, 1889:286; Noble, 1924:247 (part.); Ahl, 1931:452 (part.); Laurent, 1941a:103 (part.); 1946: 15.
Cryptothylax: Laurent and Combaz, 1950:276; Laurent, 1950d:1; Perret, 1966:448.
Leptopelis: Loveridge, 1957:316 (part.).

Type Species.—*Hylambates greshoffi* Schilthuis, by original designation.

Diagnosis.—Large frogs (snout-vent length 40–60 mm); skin shagreened; gular gland very large, obscuring gular region; vocal pouch absent.

Description.—Body slender; skin shagreened with small warts on dorsum; distal segment of digits dilated into discs; roundish digital pads surrounded by ventro-marginal groove anteriorly; transverse groove absent; vocal sac openings paired lateral slits with medial margins on ceratohyals; finger free to slightly webbed at base; toes three-fourths webbed.

Gular gland obscuring entire gular region and overlapping ventral margins of lower jaw; forearm and digital glands present, pectoral glands absent; vocal pouch absent; nuptial pad present. Pupil vertical; tympanum present.

Nasals triangular, in contact medially; dorsal exposure of sphenethmoid narrow; sphenethmoid unfused ventrally; anterior ramus of quadratojugal in contact with maxilla; frontoparietal rectangular; palatines dilated medially; prevomerine dentigerous processes and teeth present. Terminal phalanges peniform; intercalary elements completely mineralized; digital subarticular sesamoids present.

Medial margins of coracoids entire; vertebral column diplasiocoelous, not elongated; neural arches of anterior presacral vertebrae imbricate; transverse processes of eighth vertebra perpendicular to vertebral axis; sacral diapophyses moderately dilated; omosternum broadly forked at base; metasternum more than three times broader caudally than anteriorly, caudal margin serrated, stem and posteromedial portion may be mineralized; anterior horn composed of anterior (medial) and lateral processes, the latter at least one-third as long as former; alary process long, thin but broadly based; cartilaginous stalk of thyrohyal present; posterolateral process present.

M. geniohyoideus lateralis inserting on the posterior edge of the alary process; a pair of m. petrohyoideus posterior slips present; vocal sac single, made up of parallel fibers of m. interhyoideus; palmaris complex similar to that in *Hyperolius*; m. adductor longus present; one short slip of m. extensor digitorum communis longus present, inserting on proximal portion of metatarsal of third toe; m. depressor mandibulae fan-shaped, similar to that in *Hyperolius*.

Karyotype.—Undescribed.

Breeding Biology.—Amplexus and egg deposition are undescribed, although Perret (1966) has suggested that eggs are probably deposited in water or on floating plants. Voice has not been sonographed but is qualitatively described as a low sound, similar to knocking on wood. Males call from low perches near water. Tadpole is elongate and similar to that of *Kassina*, with high tail fin, but the tail fin does not extend on to back. Larval tooth formula is 1/3 or 1 + 1/3 (Lamotte et al. 1959a).

Remarks.—*Cryptothylax* are apparently common, nonarboreal dwellers of swamps, lakes, and streams in dense forest. Laurent (1976) states that they are occasionally found partially buried in the forest floor. The only described difference between the two species in the genus is size (Laurent 1976); I have not examined *C. minutus*.

Content of the Genus.—*Cryptothylax greshoffi* (Schilthuis) and *C. minutus* Laurent.

Distribution.—Forest swamps and waterways of the Congo Basin, north to Uele Province, south to west Cameroun.

Heterixalus Laurent

Eucnemis: Duméril and Bibron, 1841:528 (part.); A. Duméril, 1853:161 (part.); Duméril et al., 1854:402 (part.).

Hyperolius: Günther, 1858:85 (part.); Boettger, 1881b:508; Ahl, 1931:65.

Megalixalus: Boettger, 1881c:650; Boulenger, 1882:128 (part.); Methuen and Hewitt, 1913:56; Ahl, 1930a:524 (part.); Laurent, 1944:110 (part.).

Rappia: Boulenger, 1882:119 (part.).

Heterixalus: Laurent, 1944:111; Laurent and Combaz, 1950:277; Liem, 1970:111.

Type Species.—*Megalixalus madagascariensis* (Duméril and Bibron), by designation of Laurent, 1944.

Diagnosis.—Small to medium-sized frogs (snout-vent length 20–40 mm); pupil vertical; skin of males smooth; tympanum usually indistinct; toes usually fully webbed; posterolateral process of hyoid present.

Description.—Body gracile; skin of dorsum and limbs usually smooth; webbing of fingers reduced, toes fully webbed; digital tips dilated; gular gland a median disc oval or kidney-shaped; digital glands present in *H. betsileo*, forearm and pectoral glands absent; vocal pouch single, similar to *Hyperolius*; vocal sac openings paired anterior slits, the medial margins of which are formed by lateral process of anterior horn; tongue rounded or heart-shaped, free posteriorly; external metatarsals narrowly united; pupil vertical; nuptial pads absent, tympanum absent.

Nasals rounded, subtriangular, widely separated medially and from frontoparietals posteriorly; frontoparietals long, slightly convergent anteriorly; sphenethmoid unfused ventrally, not exposed dorsally; quadratojugal overlapped by maxilla anteriorly; premaxillaries not notched; prevomerine dentigerous processes absent; palatines somewhat dilated medially; terminal phalanges claw-shaped; intercalary elements peripherally mineralized; digital subarticular sesamoids absent.

Medial margins of coracoids entire; vertebral column diplasiocoelous, not elongated; neural arches not imbricate; transverse processes of eighth vertebra perpendicular to vertebral axis; sacral diapophyses slightly dilated; omosternum broadly forked at base; metasternum cartilaginous; 1.5–3.0 times broader caudally than anteriorly, stem partially mineralized.

Anterior (medial) and lateral processes of anterior horn present; the latter at least one-third as long as former; alary process broad-based with long stalk, width of distal dilation and base about equal; posterolateral process present, at least one-third as long as thyrohyal; cartilaginous stalk of thyrohyal present.

Third and fourth tendo superficiales able to slide through aponeurosis palmaris; vocal sac composed of posterior development of m. interhyoideus, lobe not extending posteriorly to pectoral musculature; m. adductor longus present; m. depressor mandibulae fan-shaped as in *Hyperolius.*

Karyotype.—2n = 24 in *H. betsileo* and *H. tricolor,* all metacentrics and submetacentrics of decreasing length, similar to *Hyperolius* (Blommers-Schlösser 1978).

Breeding Biology.—Apparently similar to *Hyperolius.* Calls of *H. betsileo* and *H. tricolor* have been analyzed by Blommers-Schlösser (1982). Larval tooth formula is 1/1+1,2 or 1/3 (Blommers-Schlösser 1982).

Remarks.—The genus *Heterixalus* is remarkably close to *Hyperolius.* In his generic diagnosis, Guibé (1978) mentioned only a single difference between the two: *Heterixalus* has a vertical, rhomboidal pupil; that of *Hyperolius* is horizontal. Although Liem (1970) examined a single specimen of *H. madagascariensis,* he did not provide a diagnosis; however, in Appendix 3 he listed only three differences in character states—that of pupil shape (mentioned above), insertion of the m. geniohyoideus lateralis (both taxa lack the interior slip of this muscle), and shape of frontoparietals (not supported by this study). The only differences revealed in the present work are that in the single *H. madagascariensis* available to me for clearing and staining, the posterolateral process of the hyoid is present (it is absent in all *Hyperolius* examined), and that the structure of the vocal sac involves posterior development only.

Blommers-Schlösser (1982) stated that in spite of Guibé's (1978) inclusion of five species of *Hyperolius* in the anuran fauna of Madagascar, she has never collected a single hyperoliid with horizontal pupils during her years of extensive field work there, and, in fact, she doubts that the genus is present. The difficulty of assessing pupil shape in preserved material is well known. I have examined a single male specimen of "*Hyperolius*" *rutenbergi* from Madagascar and am unable to determine the condition of the pupil. Furthermore, X-ray plates show no clear-cut differences between it and the cleared and stained *H. madagascariensis* mentioned above. At the time of writing, the hyperoliid material in the Natural History Museum in Paris, the material basis for Guibé's study, was unavailable for loan. Nonetheless, I am tentatively including the remaining hyperoliid species that Guibé (1978) placed in *Hyperolius* under *Heterixalus.* Two such species, *H. erythrodactylus* Guibé and *H. pauliani* Guibé have recently been placed in the rhacophorid genus *Boophis* (Blommers-Schlösser 1979). Additionally, *H. friedrichsi* apparently lacks a gular gland and may also be referable to *Boophis,* and *H. arnoulti* has been synonymized with *Boophis major* (Blommers-Schlösser 1982).

Content of the Genus.—*Heterixalus alboguttatus* (Boulenger), *H. boettgeri* (Mocquard), *H. madagascariensis* (Duméril and Bibron), *H. mocquardi* (Boettger), *H. betsileo* Grandidier, *H. tricolor* (Boettger) and, provisionally, *H. nossibeensis* (Ahl), and *H. rutenbergi* (Boettger).

Distribution.—Endemic to the Malagasy Republic.

Hyperolius Rapp

Eucnemis: Tschudi, 1838:35, 75 (part.); Duméril and Bibron, 1841:529 (part.); A. Duméril, 1853:161 (part.); Duméril et al., 1854:402 (part.).

Hyperolius: Rapp, 1842:289; Peters, 1855:56, 57 (part.); Günther, 1858:85; Cope, 1862:342; Hoffmann, 1873–1878: 649 (part.); Boettger, 1881:46, 47; Noble, 1824:250 (part.);

Ahl 1931:254 (part.); Laurent, 1944:115, 1950c:26, 1951c: 28; Loveridge, 1957:324; Perret, 1962:235, 1966:399; Schiotz, 1967:25, 1975:134; Liem, 1970:110.
Ixalus: Hallowell, 1844:60 (part.).
Crumenifera: Cope, 1862:343.
Rappia: Günther, 1864:130; 1868:487; Boulenger, 1882: 119 (part.), 1888:205 (part.); Nieden, 1910:59.
Hylambates: Günther, 1868:479 (part.).
Megalixalus: Boulenger, 1882:28 (part.).
Nesionixalus: Perret, 1976:29.
Type Species.—*Hyperolius marmoratus* Rapp, type by monotypy.

Diagnosis.—Small to medium-sized frogs (snout-vent length 20–24 mm); pupil round or horizontal; skin smooth in males; tympanum usually indistinct; posterolateral process of hyoid absent.

Description.—Body elongated; skin smooth; finger tips and toe tips distinctly dilated; digital pad roundish, surrounded anteriorly by a ventromarginal groove; transverse groove absent; fingers up to one-third webbed; gular gland a disc, oval, or rhomboid with lateral and posterior margins free; pectoral, forearm and digital glands present in males of some species; vocal pouch single, overlapped by gular gland, composed of folds of thin nondistensible skin; vocal sac openings paired anterior slits with medial margins formed by lateral process of anterior horn of hyoid; nuptial pads absent; pupil round or horizontal, tympanum usually absent.

Nasal triangular or squash-shaped, sometimes a distinct pointed ventroposterior process running to septomaxilla present; quadratojugal overlapped anteriorly by, but usually not in contact with, posterior part of maxilla; dorsal exposure of the sphenethmoid narrow; sphenethmoid unfused ventrally; frontoparietals rectangular, narrowly separated; palatine sometimes dilated medially; prevomerine dentigerous processes and prevomerine teeth absent.

Medial margins of coracoids entire; vertebral column diplasiocoelous, not to moderately elongated; neural arches not imbricate; sacral diapophyses slightly dilated; omosternum moderately to broadly forked at base; metasternum 1.5–3.0 times broader caudally than anteriorly, stem often mineralized medially; terminal phalanges long, slender, usually peniform but sometimes claw-shaped; intercalary elements usually peripherally mineralized in adults; digital subarticular sesamoids absent.

Anterior horn occasionally forming a complete arch, usually consisting of medial and lateral branches, the latter at least one-third as long as former; alary process with broad base; posterolateral process absent; cartilaginous stalk of thyrohyal present.

M. geniohyoideus lateralis inserting on posterior edge of alary process, sometimes additional muscle fibres inserting on hyale; m. petrohyoideus posterior consisting of two slips; vocal sac consists of anterior development of m. interhyoideus, comprising one-third of superficial mandibular musculature; third and fourth tendo superficiales able to slide through aponeurosis palmaris; the latter tendon joining the lateral half of the m. palmaris longus, third tendo superficialis joining lateral slip of medial half of m. palmaris longus; m. adductor longus present, usually inserting on distal third of m. adductor magnus; a short slip of m. extensor digitorum communis longus inserting on the proximal portion of metatarsal of third toe; pars facialis and squamosal/otic component of m. depressor mandibulae usually of equal length and width, fan-shaped, not separate.

Karyotype.—Known for about 16 species; 2n = 24, except *H. argentivittis,* 2n = 26 (Morescalchi 1968). The latter results have been questioned by Nussbaum (1980a), who pointed out that *H. argentivittis* is now considered a subspecies within the "parallelus group," others of which have been examined and found to have 2n = 24. First two chromosomes are large metacentrics, the following metacentrics and submetacentrics gradually decreasing in size (Scheel 1971, 1973; Richards and Schiøtz 1977; Bogart and Tandy 1981).

Breeding Biology.—Voices for a large number of species have not been sonographed and analyzed (Schiøtz 1967, 1975; Passmore and Carruthers 1979; and others). Qualitatively, the most common call is a single click or series of clicks, but variations are numerous and include twittering (*H. ocellatus*), bell or xylophone tones (*H. nitidulus*), trills (*H. parkeri*), creaks (*H. quinquevittatus, H. kivuensis*), buzzing (*H. alticola*) and high-pitched screams (*H. nasutus, H. pusillus* and *H. lateralis*) (Schiøtz 1967, 1975). Amplexus is axillary. Eggs vary in coloration and size, and in number from a low of 40 to over 500. Deposition is commonly in a mass of mucus on leaves or grass stems at varying height above water. *H. nasutus* deposits about 200 eggs below the surface (Wager 1965); *H. pusillus* deposits about 500 light green eggs in single layers between overlapping leaves of water lilies (Lamotte and Lescure 1977). The most remarkable reproductive behavior is that of *H. obstetricans,* described by Amiet (1974), and Lamotte and Lescure (1977), in which the females guard the eggs (deposited on a leaf overhanging water) night and day, and actually assist the tadpoles in breaking free of the viscous mucus holding the mass together. Amiet (1974) has suggested that *H. obstetricans* should be placed in a new genus, based on this behavior and on unique larval and adult features. Larval tooth formulae are 1/1+1,2; 1/3; 1/1+1,2; or 1,1+1/3. The latter is unique to *H. obstetricans.*

Remarks.—This successful genus exhibits a bewildering variety of color patterns that can vary sexually and ontogenetically. Schiøtz (1963, 1967, 1975) has used these color phases in his species analyses. As yet, however, no usable key to the genus has been completed, and in recent years none has been attempted. The species appear to be in a state of evolutionary flux; there is great overlap of external characters and a large number of geographical races of "superspecies," such as *H. viridiflavus, H. marmoratus, H. concolor,* and *H. parallellus.* Of physiological interest is the fact that *H. nasutus* can be found sitting exposed during daylight hours (J. Loveridge 1974). This species has recently been shown to be functionally "waterproof" (Withers et al. 1982), as are *Chiromantis xerampelina* (J. Loveridge 1970), and *C. petersi* (Drewes et al. 1977).

In 1976 Perret examined five specimens of *Hyperolius thomensis* Bocage housed in the Museu Bocage, Lisbon, and described them as a new genus, *Nesionixalus,* based in part on the lack of vocal sac and vocal sac openings in the males and on the oval shape of expanded toe pads. In 1978, the Museu Bocage burned to the ground, and the type series was lost. A subsequent search revealed that four specimens of this taxon remain: a male and female at the British Museum (BM 1951.1.1.91 and 98.3.30.39), and a pair at the Naturhistorisches Museum in Vienna (NHMW 3695 and 3696). A comparison of these specimens with the original description, which included photographs (Perret 1976), suggests that they are conspecific with the rather distinctive species examined by Perret. However, both males possess the typical, slitlike vocal sac openings characteristic of the genus *Hyperolius.* Inasmuch as only four specimens remain, I made no attempt to dissect the vocal sac, but from external perspective it appears to be present but reduced. Radiographs of the four specimens suggest that they are typical members of the genus *Hyperolius* and not worthy of separate generic recognition.

Content of the Genus.—At least 120 species of *Hyperolius* are presently recognized, along with myriad subspecies. The species marked with an asterisk below contain at least 7 subspecies or races: *H. acutirostris* Peters, *H. adametzi* Ahl, *H. albifrons* Ahl, *H. albofrenatus* Ahl, *H. albolabris* Ahl, *H. alticola* Ahl, *H. angolanus* Ahl, *H. argus* Peters, *H. atrigularis* Laurent, *H. balfouri* (Werner), *H. baumanni* Ahl, *H. benguellensis* (Bocage), *H. bicolor* Ahl, *H. bobirensis* Schiøtz, *H. bocagei* Steindachner, *H. bolifambae* Mertens, *H. bopeleti* Amiet, *H. brachiofasciatus* Ahl, *H. castaneus* Ahl, *H. chabanaudi* Ahl, *H. chlorosteus* (Boulenger), *H. chrysogaster* Laurent, *H. cinereus* Monard, *H. cinnamomeoventris* Bocage, *H. concolor* (Hallowell), *H. cystocandicans* Richards & Schiøtz, *H. dermatus* Ahl, *H. destefanii* Scortecci, *H. diaphanus* Laurent, *H. discodactylus* Ahl, *H. endjami* Amiet, *H. fasciatus* (Ferreira), *H. ferreirai* Noble, *H. ferrugineus* Laurent, *H. fimbriolatus* Peters, *H. friedrichsi* Ahl, *H. frontalis* Laurent, *H. fusciventris* Peters, *H. ghesquieri* Laurent, *H. granulatus* (Boulenger), *H. gularis* Ahl, *H. guttulatus* Günther, *H. horstocki* (Schlegel), *H. houyi* Ahl, *H. inornatus* Laurent, *H. kachalolae* Schiøtz, *H. kibarae* Laurent, *H. kivuensis* Ahl, *H. kohleri* Mertens, *H. krebsi* Mertens, *H. kuligae* Mertens, *H. lamottei* Laurent, *H. lateralis** Laurent, *H. laticeps* Ahl, *H. laurenti* Schiøtz, *H. leleupi* Laurent, *H. leucotaenius* Laurent, *H. lucani* Rochebrune, *H. maestus* Rochebrune, *H. marmoratus** Rapp, *H. minutissimus* Schiøtz, *H. mitchelli* Loveridge, *H. molleri* (Bedriaga), *H. montanus* (Angel), *H. nasutus* Günther, *H. nitidulus* Peters, *H. obscurus* Laurent, *H. obstetricans* Ahl, *H. occidentalis* Schiøtz, *H. ocellatus* Günther, *H. parallelus** Günther, *H. pardalis* Laurent, *H. parkeri* Loveridge, *H. phantasticus* (Boulenger), *H. pickersgilli* Raw, *H. picturatus* Peters, *H. pictus* Ahl, *H. platyceps* Boulenger, *H. polli* Laurent, *H. polystictus* Laurent, *H. protschei* Rochebrune, *H. puncticulatus* (Pfeffer), *H. pustulifer* Laurent, *H. pusillus* (Cope), *H. quadratomaculatus* Ahl, *H. quinquevittatus* Bocage, *H. raveni* Ahl, *H. rhizophilus* Rochebrune, *H. riggenbachi* (Nieden), *H. rubrovermiculatus* Schiøtz, *H. robustus* Laurent, *H. salinae* (Bianconi), *H. sankuruensis* Laurent, *H. schoutedeni* Laurent, *H. seabrai* (Ferreira), *H. semidiscus* Hewitt, *H. sheldricki* MacKay & Schiøtz, *H. soror* (Chabanaud), *H. spinigularis* Stevens, *H. steindachneri* Bocage, *H. stenodactylus* Ahl, *H. sylvaticus* Schiøtz, *H. tanneri* Schiøtz, *H. tornieri* Ahl, *H. thomensis* Bocage, *H. thoracotuberculatus* Ahl, *H. torrentis* Schiøtz, *H. tuberculatus* (Mocquard), *H. tuberilinguis* A. Smith, *H. vilhenai* Laurent, *H. viridiflavus** (Duméril & Bibron), *H. viridigulosus* Schiøtz, *H. viridis* Schiøtz, *H. wermuthi* Laurent, *H. xenorhinus* Laurent, *H. zavattarii* Scortecci, *H. zonatus* Laurent.

Distribution.—Savanna, farmbush, and forests of Africa, south of the Sahara. Probably absent from Madagascar (see *Heterixalus*).

Kassina Girard

Eremiophilus: Fitzinger, 1843:32.

Cystignathus: Duméril and Bibron, 1841:418 (part.); Duméril et al., 1854:395 (part.); Günther, 1858:26.

Kassina: Girard, 1853:421; Cope, 1865:115, Roux. 1905:785; Noble, 1924:231; Ahl, 1923:8; 1930d:277; 1931:447; deWitte, 1941:103; Laurent, 1941a:105, 1950c:1; Laurent and Combaz, 1950:273; Loveridge, 1957:320; Schmidt and Inger, 1959:183; Laurent, 1963:137; Perret, 1966:418; Schiøtz, 1967:678; Liem, 1970:104; Schiøtz, 1975:53; Laurent, 1976:31.

Hylambates: A. Duméril, 1853:161 (part.); Peters, 1855:561; Hoffman, 1873–1878:651; Boulenger, 1882:132 (part.); 1888a:205 (part.); Ahl, 1924:269; Noble, 1924:247; Ahl, 1931b:452; Laurent, 1941b:103 (part.); 1950a:1; Laurent and Combaz, 1950:271; Loveridge, 1957:320 (part.).

Cassina: Cope, 1864:182; Boulenger, 1882:31; 1888:205; Ahl, 1923:8.

Rothschildia (not de Grote, 1896): Mocquard, 1905:287.

Paracassina: Peracca, 1907:3.

Tornierella: Ahl, 1923:10; 1931:459.

Mocquardia: Ahl, 1931:330; deWitte, 1941:106.

Cassiniopsis: Monard, 1937:41.

Semnodactylus: Hoffmann, 1939:90.

Kassinula: Laurent, 1940a:314, 1941a:106.

Type Species.—*Cystignathus senegalensis* Duméril and Bibron, by monotypy.

Diagnosis.—Medium-sized to large frogs (26–70 mm); gular gland thick, oval or strap-shaped; tympanum obvious; digital tips not or but slightly dilated (except *K. parkeri*); digital subarticular sesamoids present.

Description.—Body robust; skin of dorsum and limbs shagreened; anal lobes sometimes present; distal segment of digits not or only slightly dilated (except *K. parkeri*); fingers free; toes to one-half webbed; gular gland oval or strap-shaped with lateral margins free; forearm and digital glands present, pectoral glands absent; vocal pouch single, composed of pleated, thick, distensible tissue extending caudally to include most of pectoral region, paired densely pigmented pouches present, lateral to and overlain by gular gland; vocal sac openings usually paired anterior slits associated with lateral process of anterior horn; nuptial pads absent. Pupil vertical; tympanum present.

Nasals triangular, in medial contact; quadratojugal overlapped anteriorly by, or in contact with maxillary; dorsal exposure of sphenethmoid usually narrow; sphenethmoid usually unfused ventrally; frontoparietal trapezoidal; prevomerine dentigerous processes and prevomerine teeth usually present forming two clusters behind choanae.

Medial margins of coracoids entire; vertebral column diplasiocoelous and moderately to greatly elongated; neural arches imbricate; neuropophysis of eighth vertebra moderately large; transverse processes of eighth vertebra usually perpendicular to vertebral axis; sacral diapophyses slightly to strongly dilated; omosternum broadly forked at base; metasternum cartilaginous, caudal margin variable from 0.5–3.0 times broader than anterior, stem often partially mineralized; terminal phalanges unmodified, peniform, notched, or bifurcate; digital subarticular sesamoids present; intercalary elements mineralized.

Medial and lateral branches of anterior horn present, the latter usually at least one-third as long as the former, occasionally shorter, in *K. kuvangensis* a complete arch, and in *K. cassinoides* and *K. fusca* an additional lateral process present; alary process broad-based, width of base equal to or much greater than width of distal dilation; posterolateral process absent (except in *K. wealei*); cartilaginous stalk of thyrohyal always present; alary process usually broad-based with short stalk; width of base either nearly equal to or much wider than width of distal dilation.

M. geniohyoideus lateralis inserting on thyrohyal or on posterior edge of alary process with additional slip inserting on hyale; the two posterior slips of the m. petrohyoideus posterior overlapping; palmaris musculature variable, third and fourth tendo superficiales may or may not be able to slide through aponeurosis palmaris; m. adductor longus present; one slip of m. extensor digitorum communis longus present, inserting on proximal portion of metatarsal of third digit; pars facialis and squamosal/otic element of depressor mandibulae usually distinct, the former longer and broader than the latter, pars tympanicus sometimes greatly reduced.

KARYOTYPE.—2n = 24 for *K. senegalensis* and *K. wealei*; metacentrics and submetacentrics of decreasing size. Closest to *Afrixalus* in size disparity between chromosome pairs one and two (Morescalchi 1968; Morescalchi et al. 1970; Bogart and Tandy 1981).

BREEDING BIOLOGY.—Males call from a variety of sites: from flooded meadows (Schiøtz 1963), from about 1 m up in bushes (*K. cochranae*—Colin Campbell, Ghana, pers. comm.), clinging from sedges or reeds (Channing 1976), from the water, floating on submerged vegetation (Schiøtz 1975), or from places of concealment on land (Schiøtz 1967, 1975; personal observations).

The call of most members of the genus *Kassina* is so distinctive that Schiøtz (1967) considered it a valid generic field character in West Africa. In my experience, the same holds true in east and south-central Africa. The call has been described as similar to the sound of a cork being removed from a bottle, or a drop of water falling into a full bucket, or onomatopoetically as "quoick," "hoip," or "quoip" (Wager 1965). Tandy and Drewes (*in press*) have shown that the distinctive rising characteristic of the call is due to frequency modulation, a phenomenon rare among frog calls, and that voices of the "kassinoid" species can be divided into three groups based on temporal complexity of call. The simplest (unpulsed) call is exhibited by *K. parkeri* and *K. senegalensis* of coastal Kenya (Form 3 of Schiøtz 1975 [=*K. s. argyreivittis*?]). The call of most species can be characterized as a "complex pulse train." The most temporally complex calls are those of the third group, represented only by *K. kuvangensis*, *K. wealei*, and *Kassinula wittei*. There is some evidence that *K. wealei* may in fact represent a separate genus. Most *Kassina* calls have been sonographed and analyzed and are presented in Schiøtz (1967, 1975), Channing (1976), and Passmore and Carruthers (1979).

Where deposition sites are known, eggs are deposited singly or in small groups on submerged vegetation (Wager 1965; Schiotz 1963, 1967, 1975). An amplecting pair of *K. senegalensis* captured at Lubao, western Kenya (CAS 141723 = Form 1 of Schiøtz 1975, =*K. s. ruandae*?), deposited 229 small eggs within a plastic jar.

The tadpoles of all species described to date are similar and so distinctive as to be unmistakable. They are characterized by strongly developed beaks and broad tails that extend well up onto the body. With two exceptions, the tooth formula for all *Kassina* larvae described to date (also *K. lamottei*; Drewes, unpublished data) is 1/1+1,1. The only exceptions are *Kassina maculata* and *K. wealei:* 1/3 (Wager 1965; Schiøtz 1963, 1967). Noble (1931) characterized the larvae of *K. maculata* (in part) by their possession of accessory horny plates in the lower jaw. These diagonal elements are also present in larvae of *K. decorata* (UZM 74782) and also both species of *Tornierella*.

REMARKS.—Members of the genus *Kassina* are by far the most morphologically and ecologically diverse species within any hyperoliid genus. The majority are terrestrial, nocturnal, cursorial savanna forms; however, *K. cochranae* and *K. decorata* are arboreal forest dwellers, and *K. mertensi* and *K. lamottei* are apparently forest-floor dwellers (Schiøtz 1975; Laurent 1976). Although none are truly fossorial, *K. wealei* is often found at the bottom of burrows of the cordylid lizard, *C. giganteus* (T. J. Papenfuss, University of California, Berkeley, pers. comm.). *Kassina parkeri*, recently rediscovered (Baletto et al. 1978), seems to be rupicolous, inhabiting limestone wells. Frequently, the genus *Kassina* is characterized by investigators as lacking dilation of digital tips (except *K. maculata*; see, for instance, Liem 1970); yet digital dilations are just as obvious in *K. cochranae* as in any arboreal hylid treefrog, and *K. parkeri* bears greatly expanded digital tips (that of the third digit can equal 45% of the length of the digit). The latter species is also capable of prodigious leaping, perhaps rivalling a typical ranid of equal size (Drewes, unpublished data). Although most species are found within the equatorial tropics, *K. fusca* extends well into the arid Sahel (CAS 135217–220, north of Tillaberry, Niger), and *K. parkeri* is found as far north as latitude 9° North in the Somali Horn (Baletto et al. 1978). A single male specimen of an undescribed species of *Kassina* from the Al Hills, Somalia (10 N) is in my possession.

In spite of the differences cited above, members of this genus are linked by shared, derived morphological characteristics including those of the vocal sac and gular gland of adults, mating call, and larval morphology. On the same bases, they are closely related to members of the genera *Kassinula*, *Phlyctimantis*, and *Tornierella*.

At the species level, some of the taxonomic problems remaining are the definition of members of the *K. decorata/cochranae/maculosa* complex of the forests of West Africa, and the generic status of *K. wealei* within the kassinoid genera (see Fig. 17). Additionally, Amiet (1978c) suggested that another undescribed species of *Kassina* exists in the highlands of Cameroun. The most perplexing problem in recent years, however, has been the elucidation of the *Kassina senegalensis* complex, a group of closely related savanna forms inhabiting most of Africa. Schiøtz (1975) attempted to assess *K. senegalensis* relationships in East Africa, denoting ranges for the various morphs, assigning them to "Forms 1, 2, 3, and 4" and suggesting appropriate available names for the geographic forms present should these forms be acceptable taxa. Earlier revisionary attempts have included those of Hoffman (1942), Perret (1958b), and Laurent (1976). Laurent recognized six subspecies: *K. s. senegalensis, K. s. angeli, K. s. argyreivittis, K. s. deserticola, K. s. ruandae,* and *K. s. somalica.*

Dubois has recently discovered that *Eremiophilus* Fitzinger 1843 has precedence over *Kassina* Girard 1853 (Clarke, pers. comm.). The International Congress on Zoological Nomenclature has been petitioned to grant the latter priority over the former.

Content of the Genus.—Eleven species, including *Kassina cassinoides* (Boulenger), *K. cochranae* (Loveridge), *K. decorata* (Angel), *K. fusca* Schiøtz, *K. kuvangensis* (Monard), *K. lamottei* Schiøtz, *K. maculata* (Duméril), *K. mertensi* Laurent, *K. parkeri* (Scortecci), *K. senegalensis* (Duméril and Bibron), *K. wealei* Boulenger.

Distribution.—Arid to mesic savanna, farmbush, and forests of Africa, south of the Sahara.

Kassinula Laurent

Kassinula: Laurent, 1940a:313.
Kassina: Schmidt & Inger, 1959:186; Liem, 1970:104; Schiøtz, 1975:64.
Type Species.—*Kassinula wittei* Laurent, by original designation.

Diagnosis.—Very small frogs (snout-vent length 17–22 mm); tympanum absent; nasals not ossified; m. tensor fasciae latae absent; frontoparietal fontanelle present.

Description.—Skin of dorsum and limbs smooth; digital tips not or very slightly dilated; fingers free; toes less than one-third webbed; gular gland similar to that in *Kassina*; forearm, digital and pectoral glands absent; vocal sac openings paired anterior slits, their medial margins formed by lateral process of anterior horn; tongue heart-shaped, free posteriorly; lateral metatarsals joined; pupil vertical, nuptial pads absent; tympanum absent.

Nasals triangular, not or only partially ossified, well separated medially and from frontoparietals; frontoparietals semirectangular, well separated, convergent anteriorly, a medio-posterior fontanelle present; sphenethmoid unfused ventrally, not exposed dorsally; prevomerine dentigerous processes absent, prevomer and palatine not ossified; zygomatic ramus of squamosal reduced to small nubbin; quadratojugal overlapped by maxilla anteriorly; terminal phalanges claw-shaped; intercalary elements cartilaginous, not mineralized; digital subarticular sesamoids absent.

Medial margins of coracoids perforated; vertebral column diplasiocoelous, moderately elongated; neural arches not imbricate; transverse processes of eighth vertebra angled forward; sacral diapophyses moderately dilated; omosternum broadly forked at base; metasternum cartilaginous, 1.5 times broader caudally than anteriorly, not mineralized.

Anterior (medial) and lateral processes of anterior horn present, the latter at least one-third as long as former; alary process broad-based with short stalk, width of distal dilation and base about equal; posterolateral process present, at least one-third as long as thyrohyal; cartilaginous stalk of thyrohyal present.

Aponeurosis palmaris absent, m. palmaris profundus inserts directly on third and fourth tendo superficiales proximally; m. adductor longus present; m. tensor fasciae latae absent; vocal sac musculature as in *Kassina*; m. depressor mandibulae as in *Kassina*, pars fascialis longer and broader than otic/squamosal element.

Karyotype.—Undescribed.

Breeding Biology.—Voice has been recorded by R. Keith, the sonograph appears in Schiotz (1975), and is described as a series of brief metallic clicks. Schmidt and Inger (1959) suggest that metamorphosis is completed at about 12 mm snout-vent length. Eggs, deposition site, larvae, and amplexus are undescribed.

Remarks.—This species is known from fewer than 15 examples. Based on morphology of the gular gland, vocal sac, and pouch, and other characters, *Kassinula* are clearly related to *Kassina,* *Tornierella* and *Phlyctimantis*. However, possession of a suite of unique derived features has led me to remove the taxon from *Kassina*, and return it to *Kassinula* Laurent. These characters include absence of the m. tensor fasciae latae of the thigh, possession of a frontoparietal fontanelle, absence of ossification (in adults) of the nasals (in the entire nasal area, only the septomaxillaries are ossified; Frontispiece), the prevomers and palatines, and reduction of the zygomatic ramus of the squamosal. *Kassinula* share the perforated condition of the coracoids with *Tornierella* and retention of the posterolateral process of the hyoid with *Kassina wealei*. The call of *Kassinula* differs from most of the other kassinoids; it appears to be most closely related to the calls of *K. kuvangensis* and *K. wealei* (Tandy and Drewes, *in press*). This species is clearly paedomorphic, but the developmental process responsible for this phenomenon remains obscure, as nothing is known of the ontogeny of the species. Schmidt and Inger (1959) suggested that these diminutive frogs might be high altitude forms, as most have been collected in localities above 1700 m.

CONTENT OF THE GENUS.—*Kassinula wittei* Laurent.

DISTRIBUTION.—Known only from high savanna plateaus of upper Shaba Province, Zaire, and from two localities in Zambia. I have examined the specimen in the British Museum (Natural History) from Mungwi (contiguous with Shaba Province) and confirm Schiøtz's identification (1975).

Leptopelis Günther

Hyla: HALLOWELL, 1844:193.

Polypedates: SMITH, 1850:25.

Hylambates: GÜNTHER, 1858:89; COPE, 1865:115 (part.); GÜNTHER, 1868:487 (part.); BOULENGER, 1882:132 (part.); 1888:205 (part.); NIEDEN, 1909:361 (part.); 1910:53 (part.); NOBLE, 1924:247 (part.); AHL, 1931:450 (part.).

Leptopelis: GÜNTHER, 1858:89; COPE, 1865:115; HOFFMANN, 1873–1878:649; AHL, 1924:270; NOBLE, 1924:234; AHL, 1929:185; 1931:206; DEWITTE, 1941:94; LAURENT, 1941b:91; LOVERIDGE, 1957:316 (part.); SCHMIDT AND INGER, 1959:176; PERRET, 1958a:259; 1962:235; 1966:421; SCHIOTZ, 1967:25; 1975:11; LIEM, 1970:103.

Cystignathus: GÜNTHER, 1864:481 (part.).

Pseudocassina: AHL, 1923:8.

TYPE SPECIES.—*Leptopelis aubryi* (A. DUMÉRIL), type by monotypy.

DIAGNOSIS.—Medium-sized to large frogs (snout-vent length 20–84 mm); gular gland absent in males; vocal sac openings posterior sphincters; digital intercalary elements are juvenile cartilage; m. adductor longus absent.

DESCRIPTION.—Body usually robust but occasionally slender; skin smooth or shagreened; distal segment of digits usually dilated; digital pad surrounded anteriorly and laterally by a ventro-marginal groove; transverse groove absent; fingers one-third to two-thirds webbed; gular gland absent; forearm, digital and pectoral glands usually present; vocal pouch absent; vocal sac openings are paired posterior sphincters; pupil vertical; tympanum present, nuptial pads absent.

Medial margins of coracoids entire; vertebral column diplasiocoelous, not elongated; neural arches not imbricate except in *L. brevirostris* and *L. notatus*; sacral diapophyses slightly dilated; transverse processes of eighth vertebra perpendicular to vertebral axis; nasals squash-shaped; quadratojugal in contact with or overlapped by maxilla anteriorly; dorsal exposure of sphenethmoid extensive; sphenethmoid fused ventrally; frontoparietal rectangular or slightly wider at anterior end; prevomerine teeth and prevomerine dentigerous processes present. Terminal phalanges claw-shaped, pointed; digital subarticular sesamoids absent; intercalary elements are juvenile cartilage, lacking matrix.

Omosternum unforked or occasionally notched at base; metasternum cartilaginous, 1.5–3 times broader caudally than anteriorly, usually strongly bifurcate, the medial portion of plate often mineralized; only medial branch of anterior horn present; alary process with long stalk, longer than width of base or distal dilation; posterolateral process absent; cartilaginous stalk of thyrohyal absent.

Palmaris musculature usually as in *Hyperolius* but aponeurosis palmaris absent in *L. bocagei* and *L. viridis*; m. extensor digitorum communis longus consisting of two slips, one inserting on proximal portion of metatarsal of third toe, whereas the other inserting on distal portion of metatarsal of fourth toe; m. geniohyoideus lateralis inserting on thyrohyal; m. petrohyoideus posterior consisting of three slips, the two posterior ones overlapping; vocal sac made up of posterior development of m. interhyoideus, the lobe not extending beyond anterior margin of m. supracoracoidus; m. adductor longus absent; depressor mandibulae usually similar to that in *Hyperolius*.

KARYOTYPE.—*Leptopelis* are the most karyologically variable frogs within the Hyperoliidae:

2n = 22 in *Leptopelis aubryi, L. boulengeri, L. hyloides,* and *L. viridis*; 2n = 24 in *L. bocagei, L. calcaratus, L. concolor, L. gramineus, L. palmatus,* and *L. vermiculatus*; and 2n = 30 in *L. parkeri* (Scheel 1973; Bogart and Tandy 1981). The presence of telocentric pairs suggests a closer affinity with the Ranidae than exhibited by other hyperoliid genera.

Breeding Biology.—Vocalizations have been taped and analyzed for many of the presently recognized species (Schiøtz 1967, 1975; Amiet and Schiøtz 1974; Largen 1977; and Passmore and Carruthers 1980). *Leptopelis* calls can be described as a single "clack," a "clack followed by buzzing" or "buzzing." Males call from the ground, grass stems, bushes or trees near water. Males are solitary except *L. yaldeni* (Largen 1977). Large, yolked eggs (n = ca. 50 in *L. aubryi* [Schiøtz 1963]) are buried beneath the surface of the ground near water (nest and eggs figured in de Witte 1941, and Largen 1977). Tadpoles are elongate, and have a low, long, eel-like tail which aids in migration to water after hatching (Oldham 1977). Larval tooth formula according to de Witte (1941), Schiøtz (1963, 1967, 1975), Wager (1965), Largen (1977) and Oldham (1977) is: 1,3+3/3 or 1,2+2/3.

Remarks.—*Leptopelis* seems to be fairly close to *Tachycnemis* in body size, cranial morphology, and breeding biology. However, my study indicates that it is the least derived member of the family and not related to *Tachycnemis.* Most species of *Leptopelis* are forest dwelling and arboreal; three exceptions are *L. bocagei, L. bufonides,* and *L. viridis,* all essentially savanna inhabitants. The lack of external interspecific differentiating characteristics, coupled with low sample sizes (probably because of absence of breeding aggregations) has made the alpha-taxonomy of this genus extremely difficult (Schiøtz 1967, 1975). Nevertheless, the characters treated in this study suggest that the internal anatomy of the genus is fairly uniform. One species, *L. karissimbensis,* demonstrates a classic "unken" reflex when disturbed (photographs in de Witte 1941).

Content of the Genus.—There are approximately 43 species recognized. These include *L. anchietae* (Bocage), *L. argenteus* (Pfeffer), *L. aubryi* (Duméril), *L. barbouri* Ahl, *L. becquarti* Loveridge, *L. bocagei* (Günther), *L. boulengeri* (Werner), *L. brevipes* (Boulenger), *L. brevirostris* (Werner), *L. bufonides* Schiøtz, *L. calcaratus* (Boulenger), *L. christyi* (Boulenger), *L. cinnamomeus* (Bocage), *L. fenestratus* Laurent, *L. fiziensis* Laurent, *L. flavomaculatus* (Günther), *L. gramineus* (Boulenger), *L. hyloides* (Boulenger), *L. jordani* Parker, *L. karissimbensis* Ahl, *L. kivuensis* Ahl, *L. lebeaui* (Witte), *L. macrotis* Schiøtz, *L. millsoni* (Boulenger), *L. modestus* (Werner), *L. moeroensis* Laurent, *L. natalensis* (Smith), *L. notatus* Buchholz & Peters, *L. occidentalis* Schiøtz, *L. ocellatus* (Mocquard), *L. oryi* Inger, *L. palmatus* (Peters), *L. parkeri* Barbour & Loveridge, *L. parvus* Schmidt & Inger, *L. ragazzi* (Boulenger), *L. rufus* Reichenow, *L. susanae* Largen, *L. uluguruensis* Barbour & Loveridge, *L. vannutelli* (Boulenger), *L. viridis* (Günther), *L. vermiculatus* (Boulenger), *L. xenodactylus* Poynton, *L. yaldeni* Largen.

Distribution.—Equatorial Africa, south to Natal.

Opisthothylax Perret

Megalixalus: Boulenger, 1903:63; Noble, 1924:270 (part.); Ahl, 1930c:89; 1931:422 (part.).

Heterixalus (not Laurent): Perret, 1960:373.

Opisthothylax: Perret, 1961:92; 1966:445; Schiøtz, 1967:132; Liem, 1970:112.

Type Species.—*Opisthothylax immaculatus* (Boulenger); type by monotypy.

Diagnosis.—Medium-sized frogs (snout-vent length 30–33 mm); pupil vertical; skin of dorsum and limbs very warty; gular gland of males a medioposterior disc surrounded by thin nondistensible skin of vocal pouch, not overlying it; tympanum absent.

Description.—Body gracile; digital phalanges dilated; fingers free; toes one half webbed; gular gland a medioposterior disc, margins not free; forearm and digital glands present; pectoral glands absent; vocal pouch single, composed of thin, unfolded, nondistensible skin surrounding gland, not overlain by it; vocal sac openings paired anterior slits, their medial margins formed by lateral processes of anterior horn. Pupil vertical; nuptial pad absent; tympanum absent.

Nasals triangular, equally separated medially and from frontoparietals caudally; frontoparietals rectangular; quadratojugal articulates with maxilla anteriorly; sphenethmoid unfused ventrally, not exposed dorsally; prevomerine dentigerous processes absent.

Vertebral column diplasiocoelous, not elongated; neural arches not imbricate; transverse processes relatively long, those of the eighth vertebra angled markedly forward; sacral diapophyses moderately dilated.

Medial margins of coracoids entire; omosternum greatly forked at base; metasternum cartilaginous, 1.5–3.0 times broader caudally than anteriorly, stem partially mineralized; terminal phalanges claw-shaped; digital subarticular sesamoids absent; intercalary elements mineralized.

Anterior horn consisting of anterior and lateral branches, the latter at least one-third as long as former; alary process broad-based, stalk relatively long, width of base equal to or slightly greater than width distal dilation; posterolateral process absent; cartilaginous stalk of thyrohyal present.

Third and fourth tendo superficiales able to slide through aponeurosis palmaris; vocal sac musculature composed of posterior development of m. interhyoideus, slightly bilobular, the lobes not extending caudally beyond the anterior margins of the m. supracoracoideus; m. depressor mandibulae fan-shaped as in *Hyperolius*.

Karyotype.—2n = 24, very similar to *Hyperolius, Heterixalus,* and *Phlyctimantis* except for the presence of a distinctive pair of subtelocentric chromosomes (Bogart and Tandy 1981).

Breeding Biology.—Males call from well-concealed positions from great height. Call has been sonographed and described as a deep, twice repeated click (Schiøtz 1967). Some aspects of the reproductive mode of *Opisthothylax* are unique among the hyperoliids. Amiet (1974b) discovered that *Opisthothylax* are the only hyperoliids that construct a foam nest somewhat similar to that of the rhacophorids. However, the nest is glued within a transverse fold of a leaf, a behavior similar to that of the hyperoliid *Afrixalus.* The nest is suspended several meters above flowing water and contains 6 to 10 large, yolked eggs. Tadpoles, which develop in moving water, are very small (to 25.5 mm), and quite similar to *Afrixalus* in habitus. However, the mouth is greatly reduced, and underslung, and the upper half of the beak is reduced. The larval tooth formula is 0/0 (Amiet 1974a). Major differences between the *Afrixalus* and *Opisthothylax* reproductive modes are that in *Afrixalus,* the nests include no foam, are constructed a few centimeters above or below the surface of stagnant or still water, and the tadpoles' mouths are less reduced (Amiet 1974b).

Remarks.—*Opisthothylax* are found 2 to 3 meters up in trees in dense, low altitude, swamp forests (Schiøtz 1963, 1967; Perret 1966; Amiet 1974a). Morphological characters suggest that this form is a derived arboreal hyperoliid; aspects of the breeding biology confirm its status as a separate genus.

Content of the Genus.—*Opisthothylax immaculatus* (Boulenger).

Distribution.—Southern Nigeria, south through western Cameroun, probably to Gabon.

Phlyctimantis Laurent and Combaz

Hylambates: Nieden, 1909:361 (part.), 1910:53; Noble, 1924: 247 (part.); Ahl, 1931:452, 457 (part.); Loveridge, 1941: 128 (part.); de Witte, 1941:103; Laurent, 1941a:103 (part.); Loveridge, 1957:320 (part.).

Phlyctimantis: Laurent and Combaz, 1950:271; Laurent, 1950a:1; Perret, 1966:448; Schiøtz, 1967:95; Liem, 1970:107; Schiøtz, 1975:67; Laurent, 1976:18.

Type Species.—*Hylambates leonardi* Boulenger, by original designation.

Diagnosis.—Large frogs (snout-vent length 40–52 mm); skin shagreened; hind limbs gracile; gular gland thick, disc-shaped; tympanum obvious.

Description.—Body slender; skin shagreened; dorsum with small warts; distal segment of digits dilated into discs, roundish digital pad surrounded anteriorly by ventromarginal groove; transverse groove absent; fingers free; toes half webbed; gular gland a small thick disc, free laterally and posteriorly; forearm and digital glands present, pectoral glands absent; vocal pouch single, composed of thick, pleated, distensible skin extending to pectoral region, with paired densely pigmented pockets lateral to and overlain by gular gland; vocal sac openings paired lateral slits, their medial margins formed by ceratohyals; nuptial pads present in males; pupil vertical; tympanum present.

Nasals spindle-shaped, not in contact medially; quadratojugal in contact with maxilla anteriorly; dorsal exposure of sphenethmoid narrow; sphenethmoid unfused ventrally; frontoparietal rectangular or slightly trapezoidal; prevomerine dentigerous processes and prevomerine teeth present, forming two clusters behind choanae.

Medial margins of coracoids entire; vertebral column diplasiocoelous, moderately elongated; neural arches of anterior presacral vertebrae imbricate; sacral diapophyses slightly dilated; transverse processes of eighth vertebra perpendicular to vertebral axis; omosternum broadly forked at base; metasternum 1.5–3 times broader caudally than anteriorly, caudal margin asymmetrically serrated, stem usually mineralized; terminal phalanges notched; digital subarticular sesamoids present; intercalary elements completely mineralized; anterior horn forms a complete arch, or consists of anterior and lateral processes, the latter at least one-third as long as the former; alary process broad-based, stalk short, width of base equal to or slightly greater than distal dilation; posterolateral process absent.

M. geniohyoideus lateralis inserting on posterior edge of the alary process; two slips of petrohyoideus posterior present; palmaris complex similar to *Hyperolius*; m. adductor longus present; one slip of m. extensor digitorum communis longus inserting on proximal portion of metatarsal of third toe; vocal sac single, composed of both anterior and posterior development of m. interhyoideus, anterior comprising more than one-third of the superficial mandibular musculature, the posterior extending posteriorly at least to posterior margin of m. supracoracoideus, two midlateral invaginated pockets present; m. depressor mandibulae similar to *Hyperolius*.

Karyotype.—2n = 24, metacentrics and submetacentrics of decreasing length; similar to *Hyperolius, Heterixalus*, and *Opisthothylax* (Bogart and Tandy 1981).

Breeding Biology.—Voice most similar to *Kassina* (Tandy and Drewes *in press*, sonograms of *P. leonardi* and *P. verrucosus* in Schiøtz 1967 and 1975, respectively; the voice of *P. keithae* is described qualitatively in the latter). *P. verrucosus* males call in large numbers from bushes of moderate height around stagnant forest pools (Schiøtz 1967). Tadpoles of *P. leonardi* are similar to *Kassina* but without the high tail fin. Larval tooth formula is 1/1+1,2 (Guibé and Lamotte 1958, under *Chiromantis rufescens*). In so far as is known, *P. verrucosus* is similar in all respects to *P. leonardi*, except the larval tooth formula is 1/2+2,1 (Schiøtz 1975). The breeding biology of *P. keithae* is unknown.

Remarks.—*Phlyctimantis* appear to be the least derived of the kassinoid lineage. They are closely related to *Tornierella* and *Kassina* based on adult and tadpole anatomy and on voice. Although primarily arboreal and nocturnal, they can apparently be found during the day hiding among dead leaves on the forest floor in association with the dwarf chameleon, *Brookesia* (Laurent 1976). Where present, they are apparently quite abundant (Schiøtz 1967, 1975).

Content of the Genus: *Phlyctimantis leonardi* (Boulenger), *P. verrucosus* (Boulenger), and *P. keithae* Schiøtz.

Distribution.—The three species occur in dense forests and are apparently allopatric: *P. leonardi* from Liberia east to Ivory Coast and in eastern Nigeria, western Cameroun and on Fernando Po (it is curiously absent in suitable habitats in Ghana, Togo, Benin, and western Nigeria—according to Schiøtz [1967], this is not a collecting artifact); *P. verrucosus* in eastern Zaire and Uganda; *P. keithae* is known only from the type locality, the Dabago Forest of southern Tanzania.

Tachycnemis Fitzinger

Tachycnemis: Fitzinger, 1843:31; Dubois, 1981:265.

Eucnemis: Duméril and Bibron, 1841:527 (part.); A. Duméril, 1853:161 (part.); Duméril et al., 1854:402 (part.).

Hyperolius: Günther, 1858:85 (part.); Hoffmann, 1873–1878: 649.

Megalixalus: Günther, 1868:485; 1870:150; Hoffmann, 1873–1878:650; Boulenger, 1882:128 (part.); 1888:205 (part.); Ahl, 1930a:524 (part.); 1931:422 (part.); Guibé, 1948:500; Liem, 1970:111.

Type Species.—*Eucnemis seychellensis* Duméril and Bibron, by original designation.

Diagnosis.—Large frogs (snout-vent length 60–70 mm); gular gland in males a median disc or oval; posterolateral process of hyoid present; vocal sac openings are lateral slits.

Description.—Body slender; skin of dorsum and limbs smooth; digital tips dilated; fingers half webbed; toes webbed; gular gland a median disc or oval, margins not free; forearm, digital and pectoral glands absent; vocal pouch thin, unfolded, non-distensible skin surrounding gular gland, not overlain by it; vocal sac openings paired lateral slits whose medial margins are formed by ceratohyals. Pupil vertical; nuptial pad absent; tympanum present.

Nasals large, triangular, widely and equally separated medially and from frontoparietals posteriorly; frontoparietals narrow, semirectangular, with slight, rounded lateral expansions posteriorly, strongly divergent anteriorly; frontoparietal fontanelle absent; quadratojugal overlapped by maxilla anteriorly; otic ramus of squamosal longer than zygomatic ramus, the former flattened, flangelike; prevomerine dentigerous processes absent; sphenethmoid unfused ventrally, moderately exposed dorsally; pars dentalis of premaxilla notched; palatines slightly enlarged distally.

Vertebral column diplasiocoelous, not elongated; neural arches not imbricate; transverse processes long, those of the eighth vertebra perpendicular to vertebral axis; sacral diapophyses moderately dilated.

Medial margins of coracoids entire; cleithrum wide, slightly inclined posteriorly; omosternum broadly forked at base; metasternum cartilaginous, 1.5 to 3.0 times broader caudally than anteriorly, stem partially mineralized; terminal phalanges peniform; digital subarticular sesamoids absent; intercalary elements cartilaginous, not mineralized.

Anterior and lateral branches of anterior horn present, the latter at least one-third as long as former; alary process narrow-based, width of distal dilation greater than width of base and length of stalk; posterolateral process present, less than one-third as long as thyrohyal; cartilaginous stalk of thyrohyal present.

Third and fourth tendo superficiales able to slide through aponeurosis palmaris; m. adductor longus present; vocal sac single, consisting of posterior development of m. interhyoideus, sac not extending posteriorly beyond anterior margin of m. supracoracoideus; m. depressor mandibulae fan-shaped as in *Hyperolius*.

KARYOTYPE.—2n = 24, metacentrics and submetacentrics of decreasing length, virtually identical to *Heterixalus* (Nussbaum 1980).

BREEDING BIOLOGY.—Amplexus is axillary (R. A. Nussbaum, pers. comm.; sonographs of mating calls are in his possession). According to Nussbaum (pers. comm.), *Tachycnemis* form breeding aggregations. One hundred to 500 eggs from 1 to 2 mm in diameter are deposited on the ground, or on stems of plants (such as *Dieffenbachia*), in areas soon to be flooded, or near streams or ponds. Larvae are similar in anatomy to *Leptopelis* and were briefly described by Boulenger (1909) as having very long tails (snout-vent length 18 mm, tail length 44 mm). Oldham (1977) has shown that long tails in *Leptopelis* larvae are an adaptation for terrestrial locomotion, allowing newly hatched larvae to migrate to water over damp soil. Larval tooth formula is similar to *Leptopelis*: 1,3+3/1+1,2 (R. A. Nussbaum, University of Michigan, pers. comm.).

REMARKS.—*Tachycnemis* appear to be close to *Leptopelis* in adult and larval morphology, and breeding biology, but not closely related phylogenetically.

CONTENT OF THE GENUS.—*Tachycnemis seychellensis* (Duméril and Bibron).

DISTRIBUTION.—Endemic to moist forest on a few central granitic islands in the Seychelles Archipelago.

Tornierella Ahl

Cassina: BOULENGER, 1894:644; 1895:540.
Rothschildia: MOCQUARD, 1905:288; SCORTECCI, 1930:22; PARKER, 1930:5 (part.).
Tornierella: AHL, 1923:10.
Mocquardia (not BOULENGER, 1894): LOVERIDGE, 1926:109.
Leptopelis (not GÜNTHER, 1864): PARKER, 1930:4.
Kassina: LIEM, 1970:104; LARGEN, 1975:10, 18.
TYPE SPECIES.—*Tornierella pulchra* AHL (=*Cassina obscura* BOULENGER), type by monotypy.

DIAGNOSIS.—Medium-sized frogs (snout-vent length 32–49 mm); tongue a non-emarginate disc, slightly less or slightly greater than diameter of eye; quadratojugal greatly enlarged dorsally; posterior transverse processes of vertebrae reduced.

DESCRIPTION.—Body robust; skin of dorsum and limbs smooth; two pairs of anal lobes in females; digital tips slightly dilated; fingers unwebbed; toes feebly webbed; gular gland similar to that in *Phlyctimantis*; forearm and digital glands present; pectoral glands absent; vocal pouch and vocal sac openings similar to those in *Kassina*; tongue a small non-emarginate disc, less than or slightly greater than diameter of eye. Pupil vertical; nuptial pad present but indistinct; tympanum present or indistinct.

Nasals large, triangular, in median contact, nearly in contact with frontoparietals posteriorly; frontoparietals long, rectangular; quadratojugal in contact with maxilla anteriorly, greatly enlarged dorsally; otic ramus of squamosal a horizontal flange; maxillary arch stout, deep, expanded posteriorly; pars facialis of maxilla expanded dorsally, in contact with nasal; partes dentales of maxilla and premaxilla expanded medially, bearing long, daggerlike or peg-shaped, pedicellate teeth; ventroanterior portion of sphenethmoid a single plate; not exposed dorsally; prevomers reduced and deflected dorsally; prevomerine dentigerous processes absent; palatines reduced, deflected dorsally; posterior ramus of pterygoid expanded into bony sheet enclosing angle formed by it and ventral ramus of squamosal.

Vertebral column greatly elongated, diplasiocoelous; neural arches of anterior presacral vertebrae imbricate; transverse processes of fourth vertebra expanded; posterior transverse processes greatly reduced, almost peglike; transverse processes of eighth vertebra perpendicular to vertebral axis; sacral diapophyses moderately dilated.

Medial margins of coracoids slightly or markedly perforated; omosternum moderately forked at base; metasternum cartilaginous, 1.5–3.0 times broader caudally than anteriorly; not mineralized; terminal phalanges notched; digital subarticular sesamoids present; intercalary elements mineralized.

Anterior horn a complete arch; alary process narrow-based, stalk short, less than width of distal dilation; posterolateral process absent; cartilaginous stalk of thyrohyal present.

Aponeurosis palmaris absent, m. palmaris profundus inserts directly on third and fourth tendo superficiales; m. adductor longus present; vocal sac musculature similar to *Kassina* except supramandibular extensions of m. interhyoideus present; m. depressor mandibulae similar to *Kassina,* pars facialis and squamosal/otic component separated or not.

Karyotype: Undescribed.

Breeding Biology: Voice is a typical kassinoid "boink," similar to that of most kassinoid species (Tandy and Drewes *in press*); sonograms provided in Largen (1975), males call from temporary bodies of water, supported by submerged vegetation in the manner of *Kassina maculata.* Eggs, deposition sites, and amplexus are undescribed. Tadpoles with typical kassinoid habitus, including high tail fin; an extra lower tooth row present; the tooth formula is 1/1+1,2 (Largen 1975). A pair of horny, diagonal accessory plates present, similar to those of *Kassina maculata* and *K. decorata.*

Remarks: Members of the genus *Tornierella* are closely related to those of *Kassina, Kassinula,* and *Phlyctimantis,* on the basis of adult anatomy, voice, and larval characters. Drewes and Roth (1981) have demonstrated that *Tornierella* are morphologically adapted for feeding exclusively on whole terrestrial snails and slugs; details of anatomy suggest that these species feed in a manner as yet undescribed for the Anura.

Content of the Genus: *Tornierella obscura* (Boulenger), *T. kouniensis* (Mocquard).

Distribution: Endemic to the high altitude grasslands of the Ethiopian massif, between 1700 m and 3000 m.

Appendix A. Morphological Material Examined. (C&S = cleared and double stained; SKL = skeletonized; XR = X-rayed; MUS = musculature dissected). Parenthetic quantities indicate number of specimens examined.

Hyperoliidae:

Acanthixalus spinosus: C&S (2), MUS (2)
Afrixalus brachycnemis: C&S (2), MUS (2)
A. congicus nigeriensis: C&S (1), MUS (1)
A. dorsalis: C&S (6), MUS (6)
A. fornasinii: C&S (1), MUS (1)
A. fulvovittatus: C&S (5), MUS (5)
A. osorioi: C&S (1), MUS (1)
A. quadrivittatus: C&A (2), MUS (2)
Callixalus pictus: C&S (2), MUS (2)
Chrysobatrachus cupreonitens: C&S (2), MUS (2)
Cryptothylax greshoffi: C&S (2), MUS (2)
Heterixalus madagascariensis: C&S (1), MUS (1)
H. rutenbergi: XR (1), MUS (1)
Hyperolius argus: C&S (2), MUS (2)
H. balfouri: C&S (1), MUS (1)
H. castaneus: C&S (1), MUS (1)
H. kivuensis bituberculatus: C&S (1), SKL (1), MUS (2)
H. montanus: C&S (2), MUS (2)
H. nasutus: C&S (2), MUS (2)
H. parallelus: C&S (2), MUS (2)
H. phantasticus: C&S (2), MUS (2)
H. picturatus: C&S (1), MUS (1)
H. pusillus: C&S (3), MUS (3)
H. tuberilinguis: C&S (1), MUS (1)
H. viridiflavus: C&S (2), SKL (1), MUS (2)
Kassina cassinoides: C&S (1), MUS (2)
K. cochranae: C&S (2), XR (1), MUS (4)
K. decorata: C&S (3), MUS (3)
K. fusca: C&S (1*), SKL (1), XR (1), MUS (3)
K. kuvangensis: C&S (1*), SKL (1), XR (1), MUS (3)
K. lamottei: C&S (1), XR (1), MUS (2)
K. maculata: C&S (2*), SKL (1), XR (3), MUS (3)
K. mertensi: C&S (1), MUS (1)
K. parkeri: C&S (1*), SKL (1), XR (2), MUS (2)
K. senegalensis senegalensis (Ghana): C&S (1), MUS (2)
K. s. argyreivittis (Form 3—Kenya): C&S (1), SKL (1), MUS (6)
K. s. angeli: C&S (1), MUS (1)
K. s. deserticola: C&S (2), XR (1), MUS (2)
K. s. ovamboensis: C&S (1), XR (1), MUS (1)
K. s. ruandae: C&S (1), MUS (1)
K. s. somalica: C&S (2*), SKL (1), MUS (5)
K. s. uelensis: C&S (1), MUS (1)
K. senegalensis (Form 1—Kenya): C&S (2), SKL (1), XR (1), MUS (8)
K. wealei: C&S (4), SKL (3), XR (1), MUS (7)
Kassinula wittei: C&S (1), XR (9), MUS (1)
Leptopelis brevirostris: C&S (1), MUS (1)
L. bocagei: C&S (1), SKL (2), XR (1), MUS (4)
L. boulengeri: C&S (1), MUS (1)
L. christyi: C&S (1), MUS (3)
L. hyloides: C&S (1), MUS (2)
L. karissimbensis: C&S (1), MUS (2)
L. kivuensis: C&S (1), MUS (2)
L. macrotis: C&S (1), MUS (2)

Appendix A. Continued.

L. modestus: C&S (1), MUS (1)
L. notatus: C&S (1), MUS (1)
L. viridis: C&S (3), XR (1), MUS (5)
Opisthothylax immaculatus: C&S (3), MUS (3)
Phlyctimantis leonardi: C&S (2), XR (1), MUS (2)
P. verrucosus: C&S (1), XR (1), MUS (3)
Tachycnemis seychellensis: C&S (3), MUS (3)
Tornierella kouniensis: C&S (1*), SKL (1), XR (1), MUS (3)
T. obscura: C&S (1*), SKL (1), XR (1), MUS (3)

Ranidae:

Abrana (Ptychadena) floweri:§ C&S (1*), MUS (1)
Arthroleptella lightfooti: C&S (1), MUS (2)
Arthroleptides martiensseni: MUS (1)
Arthroleptis poecilonotus: C&S (1), MUS (1)
A. reichei: C&S (1), SKL (1), MUS (1)
A. stenodactylus: C&S (1), MUS (2)
A. wahlbergi: MUS (1)
A. sp. A: C&S (1), MUS (1)
A. sp. B: C&S (1), MUS (1)
Astylosternus batesi: C&S (1), MUS (3)
A. montanus: C&S (1), MUS (3)
Aubria subsigillata: C&S (1), MUS (2)
Cacosternum boettgeri: C&S (2), MUS (3)
Cardioglossa gratiosa: C&S (1), MUS (1)
Conraua goliatha: C&S (1), XR (1), MUS (2)
Dicroglossus (Euphlyctis?) occipitalis:¶ MUS (3)
Hemisus marmoratum: C&S (3), MUS (4)
Hylarana albolabris: C&S (1), SKL (2), MUS (2)
H. galamensis: C&S (1), MUS (2)
H. lepus: C&S (1), MUS (1)
Petropedetes newtoni: C&S (1), MUS (2)
Phrynobatrachus acutirostris: C&S (1), MUS (2)
P. calcaratus: C&S (2), MUS (2)
P. graueri: C&S (1), MUS (2)
P. kinangopensis: C&S (1), MUS (2)
P. natalensis: C&S (1), MUS (2)
P. parvulus: C&S (1), MUS (2)
P. plicatus: C&S (2), MUS (2)
Ptychadena anchietae: C&S (1), MUS (2)
P. oxyrhynchus: C&S (1), MUS (1)
P. mascareniensis: C&S (1), MUS (1)
Pyxicephalus adspersus: C&S (1), SKL (1), MUS (2)
Rana amieti: C&S (1), MUS (1)
R. angolensis: C&S (4), MUS (6)
R. aurora: C&S (1), SKL (1), MUS (2)
R. (Euphlyctis?) cyanophlyctis:¶ C&S (2), MUS (2)
R. desaegeri: C&S (1), MUS (2)
R. fuscigula: C&S (1), MUS (2)
R. palmipes: C&S (2), MUS (2)
R. pipiens: C&S (2), MUS (2)
R. ridibunda: C&S (2), MUS (2)
R. ruwenzorica: C&S (1), MUS (2)
R. sylvatica: C&S (1), MUS (1)
R. temporaria: C&S (1), MUS (1)
Schoutedenella hematogaster: C&S (1), MUS (2)
S. lameeri muta: C&S (1), MUS (2)
S. pyrrhocelis: C&S (1), MUS (3)
Strongylopus grayi:† C&S (1), MUS (1)

Appendix A. Continued.

S. fasciatus mermumontanus: C&S (1), MUS (1)
Tomopterna marmorata: C&S (1), SKL (2), MUS (2)
Trichobatrachus robustus: MUS (2)

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* Plus one or more additional hyoid apparatuses.

§ *Abrana* Parker is utilized here in favor of *Ptychadena* Boulenger. Poynton (1964) argued that *A. floweri* represents just another stage in a trend toward reduction of the procoracoid bar in *Ptychadena*, and that there is no ecological data to justify recognition of a separate genus. The present study has revealed that additional differentiating characters exist from those originally described by Parker (1931); for instance, the shape of the ceratohyal in *Abrana* is different from the *Ptychadena* studied here, being more similar to the flanges present in *Cacosternum* and in a number of microhylid genera (Trewavas 1933). The specimens of *Abrana* included here were collected in sympatry with *P. anchietae*, a species very similar in appearance.

¶ Clarke (1981) found similarity between *Dicroglossus occipitalis* and the Asian *Rana tigerina*. He stated that the two may be congeneric with *Euphlyctis cyanophlyctis* (see Dubois 1975, 1976).

† The status of the genus *Strongylopus* is still in doubt, as indicated by such recent works as that of Grieg et al. (1979). However, Clarke (1981) found this species to be more derived than the closely related *Rana* and *Hylarana*, and since Channing (1979) considers *Strongylopus* distinct on the basis of morphological, ecological, and acoustical characteristics, the taxon is included here as distinct from *Rana*.

Appendix B. Character States Observed. (Character states follow observations in text. Taxa are identified in accompanying key.)

	Character States																											
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
A1	0	1	2	1	1	1	0	0	0	1	1	1	1	3	0	3	1	1	1	3	0	0	2	3	0	2	2	0
B1	0	1	3	1	0	1	1	1	1	1	1	1	1	1	0	3	1	5	1	1	5	1	1	2	0	2	2	0
B2	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	3	1	5	1	1	9	1	9	2	0	2	2	0
B3	0	1	2	1	0	1	1	1	1	1	1	1	1	1	0	3	0	5	1	1	5	1	1	2	0	2	2	0
B4	0	1	2	1	0	1	1	0	1	1	1	1	1	1	0	3	1	5	1	1	9	1	1	2	0	2	2	0
B5	0	1	2	1	0	1	2	1	1	1	1	1	1	1	0	3	1	5	1	1	5	1	1	2	0	2	2	0
B6	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	3	1	5	1	1	5	1	0	2	0	2	2	0
B7	0	1	2	1	0	1	1	1	1	1	1	1	1	1	0	3	1	5	1	1	5	1	1	2	0	2	2	0
C1	0	1	2	1	1	1	1	0	1	1	1	1	1	1	0	2	1	2	1	3	0	1	2	2	0	2	2	0
D1	0	1	2	1	0	1	0	0	1	1	1	2	1	1	0	9	1	2	1	1	4	0	2	3	0	2	2	0
E1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	3	2	4	1	2	1	1	0	3	0	2	2	0
F1	0	1	2	1	0	1	0	0	0	1	1	1	1	0	0	3	1	5	1	1	3	1	2	2	0	2	2	0
F2*	0	9	0	1	9	9	1	0	9	1	9	9	9	9	0	3	9	5	1	1	3	9	2	2	0	2	2	0
G1	0	1	0	1	0	1	0	0	1	1	1	1	1	0	0	3	1	5	1	1	2	0	2	2	0	2	2	0
G2	0	1	2	1	0	1	0	1	1	1	1	1	1	9	0	3	1	5	1	1	9	0	2	2	0	2	2	0
G3	0	1	2	1	0	1	0	1	1	1	1	1	1	1	0	3	1	5	1	1	2	0	2	2	0	2	2	0
G4	0	1	2	1	0	1	1	1	1	1	1	1	1	1	0	3	1	5	1	1	2	0	2	2	0	2	2	0
G5	1	1	2	1	0	1	0	0	1	1	1	1	1	1	0	3	2	5	1	1	2	0	2	2	0	2	2	0
G6	0	1	2	1	0	1	1	1	1	1	1	1	1	1	0	2	1	5	1	1	2	0	2	2	0	2	2	0
G7	0	1	2	1	0	1	0	1	1	1	1	1	1	1	0	3	1	5	1	1	2	0	2	2	0	2	2	0
G8	0	1	0	1	0	1	0	0	1	1	1	1	1	1	0	3	1	5	1	1	2	0	2	2	0	2	2	0
G9	1	1	2	1	0	1	0	1	1	1	0	1	1	1	0	2	1	5	1	1	2	0	2	2	0	2	2	0
G10	0	1	0	1	0	1	1	1	1	1	0	1	1	1	0	2	2	5	1	1	2	0	2	2	0	2	2	0
G11	0	1	2	1	0	1	0	0	1	1	0	1	1	1	0	3	1	5	1	1	2	0	2	2	0	2	2	0
G12	0	1	2	1	0	1	0	0	1	1	1	1	1	0	0	3	1	5	1	1	2	0	0	2	0	2	2	0
H1	1	0	0	1	0	0	1	0	1	1	3	0	0	3	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H2	1	0	0	1	0	0	2	0	1	1	1	1	0	3	0	3	0	7	1	1	6	1	0	3	0	2	2	0
H3	1	0	0	1	0	0	2	0	1	1	1	1	0	2	0	3	0	7	1	1	6	1	0	3	0	2	2	0
H4	1	1	2	0	0	0	1	1	1	1	3	0	0	3	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H5	2	1	0	0	0	0	1	1	1	1	0	0	0	0	0	3	0	6	1	1	6	1	0	3	0	2	2	0
H6	1	0	2	0	0	0	1	1	1	1	1	0	0	1	0	3	0	7	1	2	6	1	0	3	0	2	2	0
H7	1	1	0	0	0	0	1	0	1	1	9	0	0	3	0	3	0	7	1	1	6	1	0	3	0	2	2	0
H8	2	0	2	1	0	0	1	0	1	1	1	0	0	3	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H9	1	1	0	0	0	0	1	0	1	1	1	0	0	3	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H10	1	1	0	0	0	0	1	0	1	1	1	0	0	3	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H11*	1	1	2	0	9	0	2	9	9	1	9	0	0	1	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H12	1	1	2	0	0	0	1	0	1	1	1	0	0	3	0	3	2	7	1	1	6	1	0	3	0	2	2	0
H13	1	1	2	0	0	0	1	0	1	1	1	0	0	2	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H14	0	1	0	0	0	0	1	0	1	1	1	0	0	2	0	3	1	7	1	1	6	1	0	3	0	2	2	0

Appendix B. Continued.

Taxon	Character States																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
H15	1	1	2	0	0	0	1	1	1	1	1	0	0	3	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H16*	1	1	2	0	9	0	2	0	9	9	9	0	0	3	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H17	1	1	0	0	0	0	2	0	1	1	1	1	0	3	0	3	1	7	1	1	6	1	0	3	0	2	2	0
H18	2	0	0	1	0	0	2	1	0	1	1	2	0	1	0	3	1	6	1	1	6	1	0	3	0	2	2	0
H19	1	1	0	0	0	0	1	0	1	1	1	1	0	2	0	3	2	7	1	1	6	1	0	3	0	2	2	0
I1	1	1	2	1	0	1	1	1	0	1	1	2	1	0	1	3	1	6	1	1	6	1	2	1	0	2	2	0
J1	3	0	0	0	0	0	0	0	1	0	2	9	1	0	0	0	0	0	0	0	9	1	0	0	0	2	2	0
J2	3	0	2	0	0	1	0	0	1	0	2	2	1	0	0	1	0	0	0	0	3	1	0	0	0	2	2	0
J3	3	0	0	0	0	1	0	0	1	0	2	9	1	0	0	0	1	0	0	0	9	1	0	0	0	2	2	0
J4	3	0	0	0	0	1	0	0	1	0	2	1	1	0	0	0	1	0	0	0	3	1	0	0	0	2	2	0
J5	3	0	0	0	0	1	0	0	1	0	2	1	1	0	0	0	1	0	0	0	3	1	0	0	0	2	2	0
J6	2	0	2	0	0	1	0	0	1	0	2	1	1	0	0	0	1	0	0	0	3	1	0	0	0	2	2	0
J7	3	0	0	0	0	1	0	0	1	0	2	1	1	0	0	0	1	0	0	1	3	1	0	0	0	2	2	0
J8	3	0	0	0	0	1	0	0	1	0	2	1	1	0	0	0	1	0	0	0	3	1	0	0	0	2	2	0
J9	3	0	0	0	0	1	0	0	1	0	2	1	1	0	0	0	1	0	0	0	3	1	0	0	0	2	2	0
J10	3	0	2	0	0	0	0	0	1	0	2	1	1	0	0	0	1	0	0	0	9	1	0	0	0	2	2	0
J11	3	0	0	0	0	1	0	0	1	0	2	2	1	0	0	1	1	0	0	0	3	1	0	0	0	2	2	0
K1	2	1	2	1	0	1	0	0	0	1	1	1	1	1	0	3	1	3	1	2	3	1	0	1	0	2	2	0
L1	0	1	0	1	0	1	0	1	1	1	1	1	1	0	0	3	1	3	1	1	4	1	2	3	0	2	2	0
M1	1	9	0	0	0	0	1	0	1	1	1	1	1	2	0	3	1	6	1	2	6	1	0	3	0	2	2	0
M2	1	0	0	0	0	0	1	0	1	1	1	1	0	2	0	3	2	6	1	2	6	1	0	3	0	2	2	0
N1	0	0	1	1	0	0	2	0	1	1	0	2	0	2	1	2	1	6	1	1	7	1	1	3	0	2	2	0
N2	0	0	1	1	0	0	2	0	1	1	0	2	0	2	1	2	1	6	1	1	7	1	1	3	0	2	2	0

Key. A1, *Acanthixalus spinosus*; B1, *Afrixalus brachycnemis*; B2, *A. congicus*; B3, *A. dorsalis*; B4, *A. fornasinii*; B5, *A. fulvovittatus*; B6, *A. osorioi*; B7, *A. quadrivittatus*; C1, *Callixalus pictus*; D1, *Chrysobatrachus cupreonitens*; E1, *Cryptothylax greshoffi*; F1, *Heterixalus madagascariensis*; F2, *H. rutenbergi*; G1, *Hyperolius argus*; G2, *H. balfouri*; G3, *H. castaneus*; G4, *H. kivuensis*; G5, *H. montanus*; G6, *H. nasutus*; G7, *H. parallelus*; G8, *H. picturatus*; G9, *H. pusillus*; G10, *H. tuberilinguis*; G11, *H. viridiflavus*; G12, *H. phantasticus*; H1, *Kassina cassinoides*; H2, *K. cochranae*; H3, *K. decorata*; H4, *K. fusca*; H5, *K. kuvangensis*; H6, *K. lamottei*; H7, *K. mertensi*; H8, *K. parkeri*; H9, *K. senegalensis*; H10, *K. s. argyreivittis*; H11, *K. s. angeli*; H12, *K. s. deserticola*; H13, *K. s. ovamboensis*; H14, *K. s. ruandae*; H15, *K. s. somalica*; H16, *K. s. uelensis*; H17, *K. senegalensis* (Form 1); H18, *K. wealei*; H19, *K. maculata*; I1, *Kassinula wittei*; J1, *Leptopelis brevirostris*; J2, *L. bocagei*; J3, *L. boulengeri*; J4, *L. christyi*; J5, *L. hyloides*; J6, *L. karissimbensis*; J7, *L. kivuensis*; J8, *L. macrotis*; J9, *L. modestus*; J10, *L. notatus*; J11, *L. viridis*; K1, *Tachycnemis seychellensis*; L1, *Opisthothylax immaculatus*; M1, *Phlyctimantis leonardi*; M2, *P. verrucosus*; N1, *Tornierella kouniensis*; N2, *T. obscura*.

* Taxon omitted in analysis because of lack of observations of more than two character states; included in Appendix 2 for comparative purposes. For remaining taxa, missing observations (recorded above as "9") were coded as the most commonly found state of that character within the genus.

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Addendum

Since this manuscript went to press I have learned that according to Dubois (1981) the type species of *Hyperolius* Rapp is *Hyperolius horstockii* (Schlegel, 1837, p. 24) not *Hyperolius marmoratus* Rapp. Dubois (1981) has also suggested that Perret's (1962) first use of the generic designation *Opisthothylax* constituted a nomen nudum; thus the correct citation should be *Opisthothylax* Perret, 1966.